Vol. 22 No. 2

February, 1956

THE BOTANICAL REVIEW

Interpreting Botanical Progress

Cytogenetics of the Vegetable Crops. II. Crucifers.
S. H. YARNELL 81

FUTURE CONTENTS
ON INSIDE BACK COVER

Published Monthly except August and September
Box 749, Lancaster, Pa.

Entered as second-class mail matter February 4, 1935, at the Post Office at Lancaster, Pennsylvania, under the Act of March 3, 1879.

THE BOTANICAL REVIEW

Founded in 1935 by
HENRY ALLAN GLEASON and EDMUND H. FULLING
Managed, edited and published at
The New York Botanical Garden
by
EDMUND H. FULLING

Advisory Editors

PROF. CHESTER A. ARNOLD
University of Michigan
PROF. MYRON P. BACKUS
University of Wisconsin
PROF. HERBERT C. HANSON
Catholic University of America
PROF. M. M. RHOADES
University of Illinois
PROF. GILBERT SMITH
Stanford University
DR. RUSSELL B. STEVENS
National Research Council
PROF. S. F. TRELEASE
Columbia University
PROF. CONWAY ZIRKLE
University of Pennsylvania

THE BOTANICAL REVIEW is published monthly except August and September. Subscription rate for all countries is $6.00; single copies: current volume, 75¢; previous volumes, $1. All subscriptions are payable in advance at par in Lancaster, Pa., or New York. Checks should be made payable to THE BOTANICAL REVIEW.

Articles are obtained primarily by invitation. Unsolicited manuscripts are also welcome. In all cases, however, the editor reserves the right to accept, reject or suggest revisions in submitted material. All manuscripts should be on double-space typewritten pages, with references and citations in accordance with the customary style of THE BOTANICAL REVIEW.

Missing numbers can not be supplied without charge unless notice is received within two months after appearance of issues concerned.

All correspondence should be addressed to THE BOTANICAL REVIEW, at Box 749, Lancaster, Pa., or Fordham P. O., New York, N. Y.

THE BOTANICAL REVIEW

VOL. XXII FEBRUARY, 1956 No. 2

CYTOGENETICS OF THE VEGETABLE CROPS. II. CRUCIFERS.

S. H. YARNELL

U. S. Department of Agriculture, Southeastern Vegetable Breeding Laboratory, Charleston, South Carolina

Species of *Brassica* Considered 84
Cole Group 88
B. oleracea L. var. *capitata* L. Cabbage 89
Characters of the Head 89
Heading vs. Non-heading 89
Head Shape 90
Head Leaves 91
Size of Head 91
Season of Vegetative Maturity 91
Ascorbic Acid Content 91
Other Plant Characters 92
Plant Height 92
Leaf Shape and Form 92
Abnormal Types 93
Plant Colors 94
Flowers and Flowering 95
Flower Color 95
Bolting 95
Incompatibility 96
Resistance to Disease 99
Anthracnose Leaf Spot 99
Black Rot 99
Club Root 99
Downy Mildew 100
Virus Diseases 100
Yellows 101
Resistance to Insects 101
Aphids 101
Cabbage Maggot 101
Imported Cabbageworm 102
Resistance to Cold 102
Linkage 102
List of Genes 104
Cytology 105
B. oleracea L. var. *acephala* DC. Collards and Tree Kales 106
Origin and History 106
Genetics 106
Plant Characters 106
Disease Resistance 107

B. oleracea L. var. *botrytis* L. Cauliflower and Cauliflower-broccoli 107
Origin and History 107
Genetics 107
Cytology 108
B. oleracea L. var. *fimbriata* Mill. Kitchen Kale 108
B. oleracea L. var. *fruticosa* Metz. Thousand-headed Kale 108
B. oleracea L. var. *gemmifera* Zenker. Brussels Sprouts 109
B. oleracea L. var. *gongylodes* L. Kohlrabi 110
B. oleracea L. var. *italica* Plenck. Sprouting Broccoli 111
Mustard Group 112
B. nigra (L.) Koch. Black Mustard 112
B. chinensis Jusl. Pak-choi, Chinese Mustard 113
B. pekinensis (Lour.) Rupr. Pe-tsai, Chinese Cabbage 114
B. campestris L. var. *annua* Reichb. Summer Turnip-rape 115
B. campestris L. var. *biennis* DC. Winter Turnip-rape 115
B. rapa L. Turnip 116
Origin and Geographic Distribution 116
Genetics 116
Shape of Root 116
Flesh Color 117
Exterior Root Color 117
Epidermal Checking 117
Flower Abnormality 117
Bolting 118
Disease Resistance 118
Insect Resistance 118
Cytology 119
B. juncea (L.) Coss. Leaf Mustard 119
Rape Group 120
B. napus L. Rape or Swede-rape and Rape-kale 120
B. napobrassica (L.) Mill. Rutabaga or Swede 121
Genetics 121
Flesh Color 121
Exterior Root Color 122
Ascorbic Acid Content 123
Disease Resistance 123
Cytology 123
Interspecific Crosses in Brassica 124
Crosses Between Species Having Similar Genomes 124
9-Chromosome Species—The "c" Genome 124
B. oleracea–B. alboglabra and *B. cretica* 124
10-Chromosome Species—The "a" Genome 124
B. campestris–B. rapa 124
B. campestris–Oriental Species 124
B. rapa–Oriental Species 125
Crosses Between Oriental Species 125
B. rapa–B. trilocularis 126
19-Chromosome Species—"ac" Genomes 126
B. napus–B. napobrassica 126
Crosses Between Species Having Unlike Genomes 126
8- and 9-Chromosome Species and Their Amphidiploid 126
B. nigra–B. kaber 126
B. nigra–B. oleracea 127
B. carinata–B. nigra 127
B. carinata–B. oleracea 127
B. carinata–B. alboglabra 128
8- and 10-Chromosome Species and Their Amphidiploids 128
B. nigra–B. campestris 128
B. nigra–B. rapa 129

B. cernua–B. chinensis and *B. rapa* 129
B. cernua–B. campestris 129
B. cernua–B. nigra 129
B. juncea–B. nigra 130
B. juncea–B. campestris 130
B. juncea–Oriental Species 130
8- and 12-Chromosome Species 131
B. nigra–B. hirta 131
9-Chromosome Species 131
B. oleracea–B. kaber 131
9- and 10-Chromosome Species and Their Amphidiploids 131
B. kaber–B. campestris and *B. rapa* 131
B. kaber–B. pekinensis 131
B. oleracea–B. campestris 131
B. napus–B. oleracea 132
B. napobrassica–B. oleracea 133
B. napus–B. campestris 133
B. napobrassica–B. campestris 133
B. napus–B. rapa 133
B. napobrassica–B. rapa 134
B. napus–B. chinensis and *B. pekinensis* 135
B. napobrassica–B. nipposinica and *B. pekinensis* 135
B. rapa–B. oleracea 135
B. oleracea–Oriental Species 136
9- and 12-Chromosome Species 137
B. kaber–B. hirta 137
B. oleracea–B. hirta 137
10-Chromosome Species 137
B. campestris–B. tournefortii 137
B. trilocularis–B. tournefortii 137
10- and 12-Chromosome Species 137
B. chinensis–B. hirta 137
B. rapa–B. hirta 137
Crosses Involving Amphidiploid Species with Species Having Unlike Genomes 137
8- and 19-Chromosome Species 137
B. nigra–B. napus and *B. napobrassica* 137
9- and 17-Chromosome Species 138
B. kaber–B. carinata 138
9- and 18-Chromosome Species 138
B. oleracea–B. juncea 138
B. kaber–B. juncea 138
9- and 19-Chromosome Species 138
B. kaber–B. napus and *B. napobrassica* 138
10- and 17-Chromosome Species 138
B. campestris–B. carinata 138
B. rapa–B. carinata 139
B. chinensis–B. carinata 139
B. pekinensis–B. carinata 139
12- and 18-Chromosome Species 140
B. hirta–B. juncea 140
12- and 19-Chromosome Species 140
B. hirta–B. napus and *B. napobrassica* 140
17- and 18-Chromosome Species 140
B. carinata–B. juncea 140
17- and 19-Chromosome Species 140
B. carinata–B. napus 140
18- and 19-Chromosome Species 140
B. juncea–B. napus and *B. napella* 140
B. cernua–B. napella 141

Eruca sativa Mill. Rocket-salad, Rocket or Roquette 141
Raphanus sativus L. Radish 141
Origin and History 141
Genetics 142
Exterior Root Color 142
Other Color Factors 143
Other Characters 143
Incompatibility 144
Disease Resistance 144
Male Sterility 144
Cytology 145
Intergeneric Hybrids of *Raphanus* and *Brassica* 145
R. sativus–B. oleracea 145
First Generation 146
Second Generation 147
The Amphidiploid 148
Crossing Relations of the Amphidiploid 149
R. sativus–B. alboglabra 150
R. sativus–B. kaber 150
R. sativus–B. campestris 150
R. sativus–B. rapa 150
R. sativus–B. chinensis 150
R. sativus–B. pekinensis 151
R. sativus–B. carinata 151
R. sativus–B. cernua 151
R. sativus–B. juncea 152
R. sativus–B. napus 152
Crambe maritima L. Sea-kale 152
Lepidium sativum L. Garden Cress 152
Armoracia lapathifolia Gaertn., Mey., & Scherb. Horse-radish 152
Nasturtium officinale R. Br. Water-cress 153
Some General Considerations 153
Literature Cited 154

SPECIES OF *BRASSICA* CONSIDERED

Much progress has been made in recent years in defining and understanding the relationships of the cultivated and wild species of *Brassica*. This understanding has come about largely by combining studies of chromosome numbers and of behavior in the species and their hybrids with taxonomic investigations of morphology and geographic distribution.

The species and botanical varieties considered have been placed in three groups and arranged alphabetically and according to chromosome number in Table I. The cole group comprises the several botanical varieties of *Brassica oleracea* L., together with *B. alboglabra* Bailey, which may also be a variety of *B. oleracea*. The mustard group includes a rather large number of oriental and occidental species with *n* chromosome numbers ranging from 8 to 18. Two of these species, *B. kaber* (D.C.) L. C. Wheeler (charlock) and *B. hirta* Moench (white mustard), were originally assigned to

TABLE I

COMMON VEGETABLES AND SOME RELATED WILD PLANTS OF THE GENUS *Brassica*

Group and species	Botanical variety	Chromosome No.	Lit. cit.*	Horticultural type or variety	Common name in		
					English	French	German
COLE GROUP							
B. alboglabra Bailey		9	176	Kai Lan (60*)	Chinese kale		
B. oleracea L.		9	100		Cole	Chou	Kohl
" "	*acephala* DC	9	100	Ragged Jack and	Kale,	Chou vert,	Grünkohl
		9	32	Marrow kales	Borecole,	Chou	
		9	61	Cow cabbage	Tree kale,	Chou vert	
		9	161	Georgia	Collards	non pomme	Junge-kohl
" "	*botrytis* L.	9	100	Cauliflower	Cauliflower	Chou-fleur	Blumenkohl
		..	8	Cauliflower-broccoli			
" "	*capitata* L.	9	100	Red, White, and Savoy	Cabbage	Chou portager, Chou pomme	Kopfkohl
" "	*fimbriata* Mill.	9	32	Curly	Kitchen kale	Chou frises non pommes	Spargelkohl
		9	161	Dwarf Scotch			
		9	32	Dwarf Siberian			
" "	*fruticosa* Metz.	9	32	Thousand-headed	Branching bush kale		
" "	*gemmifera* Zenker	9	161		Brussels sprouts	Chou de bruxelles	Rosenkohl
" "	*gongylodes* L.	9	161	Vienna	Kohlrabi	Chou-rave, Chou-radis	Knollenkohl
" "	*italica* Plenck	9	32	Asparagus or Italian broccoli	Green sprouting broccoli	Brocoli	Brockoli
" "	*sylvestris* L.	9	176		Wild cabbage	Chou sauvage	Wildkohl

TABLE I (*Continued*)

Group and species	Botanical variety	Chromosome No.	Lit. cit.*	Horticultural type or variety	Common name in		
					English	French	German
MUSTARD GROUP							
B. nigra (L.) Koch		8	100	Alsace	Black mustard	Moutarde noire	Schwartzersenf, Senfkohl
B. kaber (D.C.) L. C. Wheeler		9	100		Charlock	Moutarde de champs	Ackersenf
(10-chromosome oriental species)							
B. chinensis Jusl.		10	100	Pak-choi	Chinese mustard, Celery mustard		
B. japonica Sieb.		10	216		Curled mustard		
B. nipposinica Bailey		10	161				
B. parachinensis Bailey		10	149		Mock Pak-choi		
B. pekinensis (Lour.) Rupr.		10	161	Pe-tsai	Chinese cabbage, Celery cabbage		
B. perviridis Bailey		10	100	Tendergreen	Spinach mustard		
(Other 10-chromosome species)							
B. campestris L.	*annua* Reichb.	10	161	Bird rape	Summer turnip-rape	Nauette d'ete	Sommerrübsen
" "	*autumnalis* DC	10	100		Winter turnip-rape	Nauette d'hiver	Winterrübsen
" "	*sarson* Prain	10	2	Kali (2*)	Sarson		
" "	*toria* Prain	10	2	Bengal mustard (2*)	Toria		
B. rapa L.		10	100	Purple-top White Globe	Turnip	Navet, Rave	Rube, Wasserrube
" "	*lorifolia* Bailey	..	...	Japanese, Shogoin	Strap-leaved turnip		

TABLE I (*Continued*)

Group and species	Botanical variety	Chromosome No.	Lit. cit.*	Horticultural type or variety	Common name in English	Common name in French	Common name in German
MUSTARD GROUP (*Cont'd*)							
B. septiceps Bailey		..	...		Seven-top turnip		
B. hirta Moench		12	100	White English	White mustard	Moutarde blanc	Weissersenf, Echtersenf
B. carinata A. Br.		17	154		Abyssinian mustard		
B. cernua Forbes & Hemsl.		18	216	Karashina (216*)			
B. juncea (L.) Coss.		18	100	Brown mustard or Chinese mustard	Leaf mustard		
" "	*crispifolia* Bailey	18	100	Southern Curled	Leaf mustard		
" "	*multisecta* Bailey	18	161		Leaf mustard		
RAPE GROUP							
B. napus L.	*annua* Koch.	19	161	Colza, Oil rape	Summer rape, Summer swede-rape	Chou colza, Colza de printemps	Kolza, Olraps, Sommerraps
" "	*biennis* (Schuebl. & Mart.) Reichenb.	19	154	Dwarf Essex	Winterrape, Winter swede-rape	Navette, Dolza d'hiver	Steckrube, Winterraps
" "	*pabularia* (DC.) Reichenb.	19	32	Asparagus kale	Rape-kale	Chou a faucher	Schnittkohl
" "		19	32	Hungary Gap			
" "	*napella* (Chaix)	19	154		Oriental rape		
B. napobrassica (L.) Mill.		19	161	Tankard	Rutabaga, Swede	Chou-navet, Navet de Suede	Kohlrube
" "	*solidifolia* Bailey	..	...	Strap-leaved	Rutabaga, Swede		

* Literature citation.

the genus *Sinapis* (280). The rape group consists of *B. napus* L. and the closely related 19-chromosome species *B. napobrassica* (L.) Mill.

The assumption that morphological similarities and diversities accurately reflect the degree of genetic relationship contributed much to the earlier confusion. In the botanical varieties of *B. oleracea*, the genetic relationships have turned out to be closer than their great morphological diversity seemed to warrant. Just the reverse of this is illustrated by the use of the term "kale" to include similar varieties in the 9-chromosome *B. oleracea* and the 19-chromosome *B. napus*. The cytogenetic basis for this error was disclosed when it was found that *B. napus* must have originated as an amphidiploid of a cross between *B. oleracea* and *B. campestris* L. The use of the term "rape" for types of *B. campestris* and *B. napus* is explained in the same way.

Within each of the three groups—cole, mustard, and rape—species with the same chromosome number cross rather readily. Compatibility and other genetic factors influence crossability, so that results of interspecific crosses depend to some extent upon the botanical or horticultural varieties of each species used in the cross. Crosses between species differing in chromosome number have usually been more successful where the species with the higher chromosome number was used as the seed parent. In wide crosses, rather large numbers of pollinations have been needed to demonstrate the degree of crossability.

It is not implied that there are no further problems for a complete understanding of the relationships of the different forms of *Brassica* or that there are now no differences of opinion on these matters. Nevertheless the basic outline has been established. The degree of detail achieved will be apparent in the discussion of the species and their crosses.

COLE GROUP

The nine cultivated forms of *B. oleracea* considered here were long thought to be derived from a single wild form, *B. oleracea* var. *sylvestris* L., native to the coasts of western and southern Europe and adjacent islands (9). Most of these botanical varieties have been in cultivation for so long, there is no definite information in regard to their origin. No cytological difference was found

between wild plants collected in England and the cultivated coles (29). There are several 9-chromosome wild cole-like species that may have contributed to the cultivated forms now included in *B. oleracea.* Among these may be mentioned *B. balearica* Pers. (135), *B. cretica* Lam. (63), *B. insularis* Moris (31) and *B. rupestris* Raf. (135).

B. oleracea L. var. *capitata* L. Cabbage

Cabbage is discussed first because of its commercial and experimental importance. Savoyed cabbage, sometimes referred to as var. *sabauda* L., is considered as belonging to this group. A review of early literature led Henslow (75) to conclude that modern cabbage was developed in Europe during the sixteenth century.

CHARACTERS OF THE HEAD

HEADING VS. NON-HEADING. The distinguishing character of cabbage is the development of numerous wrapper leaves surrounding the terminal bud. These are usually tight enough to form a head, or " heart ". Reports of crossing between heading and non-heading forms are not in full agreement (3, 41, 43, 76, 111, 134, 183, 208, 231, 255). This is the result partly of the use of different materials, which have different degrees of heterozygosity, and partly of the difficulty of defining " heading " and " non-heading " in segregating generations, where variation between the two parental types may be continuous. Whether or not any factors for heading are considered to be dominant seems to depend upon the degree of looseness permitted within a classification of heading. All workers assume some or all factors to be recessive. The simplest proposal (183) calls for two recessive factors, $n_1n_1n_2n_2$, for heading. This is based on a cross between cabbage and kale. The F_1 had no more than a faint indication of heading—a rosette with incurved leaves. Both parental forms were recovered in the second generation, with continuous variation between the two extremes. $N_1N_1n_2n_2$ and $n_1n_1N_2N_2$ are considered to give the same effect as $N_1n_1N_2n_2$. Similar results were obtained in a cross between cabbage and kohlrabi (183). The backcross to cabbage on this basis gives 1 $N_1n_1N_2n_2$ (very slight heading) : 1 $N_1n_1n_2n_2$: 1 $n_1n_1N_2n_2$ (both slight heading) : 1 $n_1n_1n_2n_2$ (heading). Two backcross families totaled 72 : 141 : 66. The backcross to non-heading should

give a 3:1 ratio for non-heading and very slight heading. Back-crosses of Savoy cabbage-kohlrabi and -curly kale to the non-heading parent totaled 277 non-heading to 85 with a slight tendency to head. The author (183) concedes that there may be also minor modifying factors.

Other work (3) involving cabbage and kitchen kale led to the proposal of one dominant major and three minor recessive factors for heading, $KKk_1k_1k_2k_2k_3k_3$. The first generation had 1 plant that was definitely heading, 26 with a tendency to head, and 4 plants with a slight tendency to head. The second generation of five such crosses totaled 562 heading (including loose heads) and 168 non-heading. This demonstrated the effect of the major dominant gene. The factor combination $KkK_1K_1K_2K_2K_3K_3$ gives a very loose head according to this scheme. The recessive factors have a cumulative effect for increased tightness of head.

In general, an intermediate condition exists in the first generation of crosses between cabbage and the non-heading botanical varieties of *B. oleracea.* Because both heading and non-heading types are obtained in the second generation, most workers think that a relatively small number of genes are involved. Malinowski (134) and also Sampson (208) suggest three. Kristofferson's results (111) are somewhat exceptional in that he obtained only one per cent heads in a cabbage-kale F_2 population of 14,000 plants. He concludes that there are probably a good many factors for heading. The choice of the non-heading parent may help to explain these results. There is a greater genetic difference with respect to heading between cabbage and its wild relative *B. oleracea* var. *sylvestris* (76) than between cabbage and brussels sprouts (134). The cross between tight-headed cabbage and the looser headed Savoy type supports the assumption that the factors favoring a normally tight head are recessive (196). The first generation of this cross was nearer the Savoy parent in this respect, and the second generation also lacked the tightness of the cabbage parent. An effect of the environment on head tightness will be discussed in connection with flowering.

HEAD SHAPE. Cabbage heads may be classified as flat, round or pointed. There are also intermediate shapes. Round-headed varieties often tend to be oblate. Tschermak (255) reports pointed to be dominant to round. Segregates of this type of cross may be

blunt-pointed or triangular in shape. Many genetic factors are involved in determining shape of head (43, 128). Pearson (182) divided width by length to give a shape index. This varied among inbred lines from 0.9 (long) to 1.37 (flat). In crosses between inbred lines the index was often intermediate, but in one case it was the same as the flat parent, and in another the F_1 was flatter than either parent.

HEAD LEAVES. The number of non-wrapper leaves attached to the main stem below the head proper varies from a few to as many as 25 (182). In crosses between lines with few and those with many non-wrapper leaves, the former condition is dominant. There are modifying factors.

SIZE OF HEAD. Inbreeding in some cases does not reduce the size of head; in other cases head size may be reduced in different amounts (114, 182). Crosses of unrelated lines, such as smooth cabbage × savoy, may have heads larger than those of either parent (196).

SEASON OF VEGETATIVE MATURITY. In crosses between early and late maturing varieties, the first generation is nearer the early parent (196). In crosses between unrelated lines, the F_1 plants are earlier than either parent when compared in adjacent rows the same season (179). This is regarded as an expression of hybrid vigor. In such cases the F_1 heads are larger than those of the parents. In the same way early lines of smooth cabbage × savoy produce a first generation that is earlier than either parent (196). There are also genes for earliness (179).

ASCORBIC ACID CONTENT. The vitamin-C concentration is one of those characters on which both genes and environment have an important influence. In the following discussion all data for ascorbic acid are in terms of milligrams per 100 grams of fresh sample. Heavy applications of nitrogen and of a complete fertilizer favor high ascorbic acid (24). The effect of season may vary the readings as much as 40 points (21). The amount of sunlight, rainfall and temperature also contribute to the amount of ascorbic acid present (159). Varieties with smaller heads tend to have a higher concentration than those with larger heads (21, 187). In general, closely related lines may vary rather widely. Partly because of this and partly because of environmental influ-

ence, the results of different workers may not be in close agreement. For example, representatives of the Copenhagen Market group of varieties have been listed as low (21), both low and high (65), and intermediate (71, 224) in ascorbic acid, while Wisconsin Hollander and Resistant Red Hollander were low and high, respectively, in the same test (224). This implies heterozygosity for genes affecting the content of ascorbic acid and the possibility of improvement through selection. Crosses between lines that are low and high in ascorbic acid give a first generation that is intermediate (272). The second generation follows a normal curve in this respect. Several genes are thus involved.

OTHER PLANT CHARACTERS

PLANT HEIGHT. Plant height, like head size, may be affected in crosses that involve hybrid vigor (118). In addition, plant height is influenced by several specific genetic factors (118). The greatest amount of variation obtained in the third generation of a cross between tall and short was 7.80 to 13.61 inches. Tallness is dominant to shortness (134). There is a major gene for height, designated *T t* (183). Most varieties of cabbage are recessive in this respect, although some carry the dominant allele. Several commercial varieties occasionally segregate a dwarf form that is recessive to normal (285). This type is too small to form a head.

LEAF SHAPE AND FORM. There is a single major factor difference between cabbage and kohlrabi for leaf width (134, 183). Cabbage has the dominant gene *W* for wide leaf. There are modifying factors.

Cabbage typically has a sessile entire leaf at the mature vegetative stage in contrast to the petiolate lyrate leaf of the vegetatively mature kohlrabi. Two closely linked factors are responsible: *Pet* (originally *P*), producing a petiolate leaf, and *En* (originally *E*), producing an entire leaf. Cabbage is thus *pet pet En En*, and kale and kohlrabi are *Pet Pet en en* (183). The cross produces plants with petiolate entire leaves, *Pet pet En en*. Brussels sprouts are *Pet Pet En En*. The double recessive *pet pet en en*, producing a sessile lyrate leaf, has been found in the segregating second generation but apparently has never become established in any of the related vegetable crops. Unpublished data secured at the U. S. Southeastern Vegetable Breeding Laboratory require the presence

of modifying factors for explanation. The degree of development of the lamina along the basal part of the midrib varies widely; in some varieties and under some conditions it is fully developed to the point of attachment of the leaf to the stem, while in others a substantial part of the midrib is so devoid of lamina as to appear definitely petiolate. The term "sessile", however, appears correct in describing the typical leaf of the heading types of cabbage. Allgayer (3) found an intermediate, lobed condition of the petiole to be dominant, but did not establish the number of genes involved.

The crinkled or rugose leaf of savoy cabbage is largely dominant over smooth (255). In the second generation, 10 of 780 plants were as smooth as the smooth-leaved cabbage parent (196). Likewise there were very few fully savoyed plants in the second generation of Kwan's cross (118). The last author suggests complementary factors, *W* and *S*. The double recessive produces smooth leaves. He thinks there may be additional modifying factors. In the second generation of Drumhead Savoy × collard and the reciprocal cross, Price (191) secured 397 plants, all of which were savoyed in some degree.

The difference between the non-curly cabbage leaf and the curly leaf of kale is polygenic (134). Leaves of the first generation are somewhat nearer to the leaves of cabbage. The second generation displays a continuous variation that may be asymmetrical. In addition to the types in the parents, Pease (183) provides three intermediate grades of increasing curliness. He gives the following F_2 data: 85 smooth: 1268 grade I: 2614 grade II (same as the F_1): 101 grade III: 1 curly. Many factors are obviously involved.

The presence of bizarre protuberances on the leaves was known to the ancient Greeks, who called the form "asparagodes" (183). It is said to result from the presence of the dominant or partially dominant gene *A* (183). It is suggested that this be changed to *As* to avoid confusion with the basic color factor *A*. Experience at the U. S. Southeastern Vegetable Breeding Laboratory suggests either a major effect of the environment or a more complex genetic explanation.

ABNORMAL TYPES. As with other plants, continued inbreeding has brought to light a number of abnormal types. In cabbage practically all of these genotypes interfere seriously with head formation. Detjen and McCue (43) discuss and illustrate a num-

ber of these. They include several rosette types (zinnia, dwarf and tall saucer, narrow spindle and others), early cauliflower, which bears a crude resemblance to cauliflower, fasciated plants, and various flower irregularities. All of these appeared in inbred Volga. Certain crosses involving Volga, which were then inbred, have uncovered notch, dwarf, balloon rosette, flat rosette, whiptail, which is similar in appearance to the nutritional defect in cauliflower, (285) and several as yet unreported abnormal types mostly lacking in vigor. The inheritance of none of these has been fully determined. One of these under study at the U. S. Southeastern Vegetable Breeding Laboratory has very irregular leaf margins, simulating severe insect injury. The two can be distinguished on close examination. This type is genetically related to notch. It is occasionally seen in illustrations (110).

PLANT COLORS. Two factors are responsible for red cabbage. *A*, a basic color factor, has no effect alone, but with *D* it produces a red leaf (111, 134, 183). The gene *B* alone results in a light-red midrib, and with *A* gives a dark-violet midrib. The factor *C* alone is colorless, but with *A* also gives a dark-violet midrib (111, 134). Another gene, *E*, extends the area of the dark-violet color. *B* and *C* together have the same effect as *B* alone (111). Red cabbage is *DAbce*, and green cabbage may be *daBCE*. This form has light-red midrib. Not explained by the above genetic formulas are Allgayer's results (3). He obtained a second-generation segregation of 235 colored blade : 358 colored midrib : 166 green. Because this approximates a 1 : 2 : 1 ratio, he proposed a single gene, *P*, to give a colored blade when homozygous and only colored veins when heterozygous. This is not the equivalent of Kristofferson's *D* (111).

The gene *M* produces magenta, and *S* sun color (129). Combined they give purple; the double recessive is green. Kwan (118) later showed that sun color results from duplicate genes, R_1 and R_2. A cross between deep purple and sun color has 15 purple to 1 sun color in the F_2 generation. Kristofferson (110) crossed a white cabbage with kale and got in the second generation 9 dark reddish violet : 3 clear red : 4 white. This corresponds to Kwan's cross (118) of deep-purple × green, which gave 9 purple : 3 sun color : 4 green in the second generation. He considers this genetically distinct from the preceding sun color and proposes *GH* for deep pur-

ple, *Gh* for sun color, and *gH* and *gh* for green. Neither of Kwan's crosses involving sun color reproduces the results of Magruder and Myers (129).

Magruder (127) found a pinkish color in the bud of an introduced line (P.I. 82649). This segregated 84 colored to 32 white in the second generation.

FLOWERS AND FLOWERING

FLOWER COLOR. The flowers of cabbage are ordinarily yellow. An occasional white mutation appears. When this is crossed to yellow, there is a 1 : 1 segregation in the first generation (26, 97). The same simple dominant white flower in other coles has been designated *Wh* (177).

BOLTING. The cabbage plant is a biennial, normally blooming the second season. After it has reached vegetative maturity, a period of about 60 days below 40° F. is usually required to initiate flower bud development (139). It has been shown that many varieties respond in the same way to an equivalent amount of cold after the main stem of the plant exceeds the diameter of a pencil (18, 19). This circumstance is not important in the commercial summer crop in the northern United States and other regions providing uninterrupted growth, or in the production of the fall crop in the South, since there is little or no opportunity for effective cold after the plant has reached this critical stage of development. In the spring crop in England (134, 183, 232) and in the southern United States (287), if plants become too large before the onset of cool weather, entire commercial fields may bloom instead of producing heads. Rather wide genetic differences exist among strains and varieties in regard to this response to cold. Many summer and fall varieties, such as Copenhagen Market, may become a total loss as a spring crop under conditions favorable for flowering, while under identical environmental conditions the widely planted Early Round Dutch may not show a single seed stalk. Under conditions favoring bolting in Virginia, 15 strains of Early Round Dutch bolted 4.7 to 25.3 per cent (287). Strains of Charleston Wakefield bolted 14 to 31.3 per cent. Different breeding lines grown for a spring crop at the U. S. Southeastern Vegetable Breeding Laboratory have varied as much as 90 per cent in the proportion of plants flowering under such conditions.

Non-bolting is reported to be a simple dominant (134, 207, 232). Apparently modifying factors determine the proportion of plants bolting.

A condition related to blooming has been reported for plants maturing during January in Louisiana (140). Plants maturing at this time have reached a stage during November and December that is responsive to cold. If the cold is of sufficient duration to initiate flower bud formation, the core tends to elongate, even though heads of normal size are formed. This results in a somewhat loose or "puffy" head. Varieties differ in their response to these conditions. The percentages of puffy heads follows: Louisiana Copenhagen, 9.7; Charleston Wakefield, 18.7; Copenhagen Market, 25.8; Succession, 27.5; Danish Ballhead, 29.2; All Head Early, 38.6. The condition has been noted in other parts of the southern United States.

A new vegetable called "caulicab" has been reported (263). It is said to be an accidental cross between broccoli and cabbage. When planted for fall production small heads are formed. When caulicab is grown for spring harvest buds develop within the outer leaves. There is no segregation. The situation appears to be somewhat similar to that of the cabbage mentioned in the preceding paragraph.

INCOMPATIBILITY. "Incompatibility" is a term applied to a marked reduction or absence of seed development in certain controlled self- and cross-pollinations compared with the seed formation after open pollination. It differs from "sterility" in that the functional parts of the flower and its gametes are morphologically normal, while sterile plants usually exhibit some degree of chromosomal or morphological deterioration. The degree of incompatibility may be influenced genetically and by the environment, internal and external. Incompatibility is rather common in cabbage, and both male and female sterility have been reported as well (42).

Incompatibility results from a reduction in the normal rate of growth of the pollen tube in the style, which prevents fertilization and subsequent development of the seed. The simplest genetic explanation, known as the "oppositional hypothesis", assumes that pollen carrying a gene for incompatibility, which is also found in the style, will be unable to function normally. A considerable

allelic series of these factors, designated s_1, s_2, s_3, s_4 and so on, provides the basis for rather wide inter-compatibility among self-incompatible plants. Plants carrying the factors s_1s_2, for example, are self-incompatible and incompatible with other s_1s_2 plants, but cross-compatible with all other genetic combinations, such as s_1s_3, in which only the s_3 pollen functions. This results in s_1s_3 and s_2s_3 progeny. The results of reciprocal crosses may be unlike where one plant is homozygous and the other heterozygous. For example, $s_1s_1 \times s_1s_2$ is compatible because the s_2 pollen functions normally, while $s_1s_2 \times s_1s_1$ is incompatible because all pollen carries a factor for incompatibility that is found in the female. In similar manner reciprocal crosses between plants with a single incompatibility factor in common give dissimilar genetic results. Thus $s_1s_2 \times s_1s_3$ gives both s_1s_3 plants and s_2s_3 plants, while $s_1s_3 \times s_1s_2$ gives s_1s_2 and s_2s_3 plants in a 1:1 ratio. In both instances s_1 pollen is excluded and only its allele functions. In the direct cross this is s_3 and in the reciprocal it is s_2.

The work of Kakizaki (98) is somewhat more complex. In addition to the situation described in the preceding paragraph, he reports a second allelic series of genes, T_1, T_2, etc., at a different locus, that favors pollen tube growth. The "s series is epistatic to the T series, but the T in double dose is more active than the s in simple dose" (98, page 169). Kakizaki assumes that the different members of each series have different degrees of effectiveness. An interesting feature of this arrangement is that self-compatible plants always segregate the two types in equal numbers. Some self-incompatible plants breed true for incompatibility, while others segregate 1 compatible to 3 self-incompatible. Five genetic types were found among ten plants of the variety Succession. They were $s_1s_1T_1T_2$, $s_2s_3T_1T_2$, $s_1s_2T_1T_2$, $s_1s_3T_1T_1$ and $s_1s_3T_2T_2$. Seven genetic types were among ten plants of the variety Toyodawase. They were $s_1s_2T_1T_2$, $s_2s_3T_1T_2$, $s_1s_3T_1T_2$, $s_1s_1T_1T_2$, $s_1s_2T_1T_1$, $s_1s_2T_1T_1$ or $s_1s_2T_2T_2$, and $s_2s_3T_1T_1$ or T_2T_2. The following will illustrate the behavior of the genotypes: s_1 can not pollinate $s_1s_1T_1T_1$ or $s_1s_1T_2T_2$ but can pollinate $s_1s_2T_1T_1$ or $s_1s_2T_2T_2$. Neither s_1 nor s_2 can pollinate $s_1s_2T_1T_2$, but both s_1 and s_3 can pollinate $s_1s_3T_1T_1$ or $s_1s_3T_2T_2$. The reason that a self-compatible plant such as $s_1s_3T_1T_1$ always segregates compatible and incompatible plants in equal numbers is that both the homozygous forms,

$s_1s_1T_1T_1$ and $s_3s_3T_1T_1$, are self-incompatible, while the heterozygous $s_1s_3T_1T_1$ plants are self-compatible.

Mizushima and Katsuo (143) extend the oppositional hypothesis on the assumption that cabbage, because of observed secondary association, is considered to be a modified tetraploid and therefore must contain duplicate genes for incompatibility. They propose two allelic series, *Sp* and *Sq*, each of which has up to three genes—Sp_1, Sp_2, Sp_3 and Sq_1, Sq_2, Sq_3. Each pollen grain contains one of each, for example, Sp_1Sq_2, either of which when present in the style of the female parent prevents fertilization. Five self-incompatible plants of the variety Summer were found to fall into three genetic groups as follows: A—$Sp_1Sp_2Sq_1Sq_2$, B—$Sp_1Sp_1Sq_1Sq_3$, and C—$Sp_1Sp_3Sq_1Sq_3$. Gametes for each are A—Sp_1Sq_1, Sp_1Sq_2, Sp_2Sq_1, and Sp_2Sq_2, B—Sp_1Sq_1, and Sp_1Sq_3, and C—Sp_1Sq_1, Sp_1Sq_3, Sp_3Sq_1, and Sp_3Sq_3. A × B is incompatible because all male gametes carry Sp_1. B × A is compatible because Sp_2Sq_2 gametes function normally in styles of B. A × C is compatible because Sp_3Sq_3 pollen can function. C × A permits Sp_2Sp_2 pollen to grow normally. Both B × C and C × B are incompatible because each group contains Sq_1Sq_3. It is possible that Pearson's results (178) can be placed in this general category.

There is evidence (241) that reduced germination of pollen on the stigma of an incompatible cross may contribute to the result. For example, only 32.2 per cent of the pollen had germinated after eight hours on self-pollination of Succession, while 72.2 to 81.8 per cent had germinated during the same period after interpollination.

Incompatible pollinations are often successful when the bud is pollinated one to three days before the flower reaches anthesis. The use of green self-incompatible and cross-compatible purple plant types provides an accurate measure of the proportions of pollen from self- and cross-pollination of the same flower that are successful in completing fertilization (5). After pollinating with a mixture of self pollen from the green plant plus outcross pollen from a purple plant at different intervals before anthesis, the following percentages of purple plants were obtained: four days—35.29 to 54.12, three days—25.9 to 54.12, two days—34.9 to 62.0, one day—50.98 to 92.68, and when pollinated the day of anthesis—75.0 to 92.17. It is concluded that at the earlier bud stages the

material in the styles responsible for a reduction in the rate of growth of tubes from incompatible pollen had not yet fully developed. A few cases have been found in which pseudo-fertility-modifying genes have considerably reduced the effectiveness of the *s* factors (6).

RESISTANCE TO DISEASE

ANTHRACNOSE LEAF SPOT. Some cabbage has resistance to anthracnose leaf spot, caused by *Colletotrichum higginsianum* Sacc. (211). The degree of resistance is less than that in Southern Giant Curled leaf mustard, and it is greater than the resistance to this disease in broccoli and kale.

BLACK ROT. The variety Houser was reported resistant to black rot as far back as 1908 (46). At that time it was considered to be " practically immune under field conditions " in Ontario. More recently (247) various degrees of resistance were recorded as per cent of healthy plants—Late Giant, 59.7; Early Drumhead, 31.2; Early Sugarloaf, 19.4; " Yellows Resistant ", 22.2; and Roem van Enkhuizen, 12.5. Inoculation of seedlings with the causal organism, *Xanthomonas campestris* (Pam.) Dows., demonstrates varying degrees of susceptibility. The data are presented (11) as per cent of seedlings showing symptoms of the disease after 43 days: Jersey Wakefield, 13.1; Allhead Select, 14.3; Savoy Chieftain, 24.4; Charleston Wakefield, 32.6; Huguenot, 38.8; Resistant Glory, 62.0; Globe, 65.8; Mammoth Red Rock, 74.6. Certain selections of Huguenot had less than 5 per cent infection, and Early Fuji and Houser had 5.0 and 4.8 per cent, respectively. Later tests with inbred Huguenot and Early Fuji (12) support these findings of high resistance to black rot. Commercial varieties classified as resistant after water inoculation in Florida (45) are Red Acre, Penn State Ballhead C, All Head Select, Wisconsin Bugner, Florida Danish and Savoy Perfection Drumhead.

CLUB ROOT. Tests conducted in Germany (204) demonstrated that, while rutabaga is immune from club root, caused by *Plasmodiophora brassicae* Wor., the varieties of cabbage tested were completely susceptible. More recently three German varieties, Bohmerwald, Bindsachsener and Muhlviertler, were shown to carry resistance (62). They had 46.1 to 55.6 per cent of healthy

plants. Severe infection of 15 Russian varieties reduced the yield by 50 per cent (49). No varietal differences in susceptibility were observed after artificial inoculation, but there appeared to be varietal differences in susceptibility to natural infection. A recent comparison of Russian varieties with other European varieties (117) indicates a higher degree of resistance in the former. The early variety Valjvatjevskaja was least susceptible. Its cross with Nomer Pervyi was less resistant. A severe greenhouse test of 2600 plants of 25 varieties of cabbage in Wisconsin (269) yielded only three plants free of infection. A cross between cabbage and kale was resistant to club root (273). After self-pollinating four times, resistant non-heading plants were backcrossed to cabbage. Resistant heading plants were obtained in the second generation of the backcross. Good resistant cabbage types were selected from the fifth generation (274). A second backcross to cabbage was necessary for Marion Market, Resistant Charleston Wakefield and All Head Select. Susceptibility is completely dominant in crosses between highly susceptible and highly resistant. Ten to 20 per cent of the second generation are resistant, indicating polygenic inheritance. In this work (274) resistance to club root was satisfactorily combined with resistance to yellows.

DOWNY MILDEW. The disease, referred to as " rust " by growers in the South, is caused by *Peronospora parasitica* (Pers. ex Fr.) Fr. No resistance was found in American varieties of cabbage to this organism as it occurs in Mississippi (51, 52). Resistance is reported (278) to two varieties of the organism—to race 2 of var. *brassicae* and to var. *raphani*. Resistance is of the type in which the host cells surrounding the point of infection are killed, thus blocking further progress of the disease.

VIRUS DISEASES. The turnip virus 1 (virus A) and the cauliflower virus 1 (virus B) attack cabbage individually and in combination (188). Resistance to both is partially dominant, probably with polygenic inheritance (190). Because of this, resistance in most varieties can be developed through selection. As might be expected from this type of inheritance, resistance is incompletely dominant in crosses with susceptible. There may be some linkage between genes for resistance to viruses A and B (190). Varieties listed as carrying resistance to these mosaic viruses are Wisconsin All Seasons, Wisconsin Ballhead, Wisconsin Hollander, Globe,

Stein's Early Flat Dutch, All Head Select and Succession (120, 188, 190). In New York resistance to these viruses is reported (164) in Geneva Resistant Domestic 140 and Selected Danish (Klitgord). Some cabbage is resistant to a mosaic disease of rape and other cultivated crucifers found in China (123). Cabbage and other coles, except sprouting broccoli, may have resistance to T_1 and T_6 turnip mosaic viruses (121). Cabbage, cauliflower, Dwarf Scotch Curled kale and brussels sprouts may carry resistance to the T_9 strain.

YELLOWS. Selection for resistance to yellows, caused by *Fusarium oxysporum* Schlecht f. *conglutinans* (Wr.) Snyd. and Hans., in commercial fields in Wisconsin reduced the loss from this cause within a few years from about 84 to 20 per cent (88, 89). A single dominant gene for resistance was found in All Head Early, Copenhagen Market and in Glory of Enkhuizen (*266, 267, 268, 276, 277*). This apparently is derived directly from *B. oleracea sylvestris* L. (*267, 277*). There is also a polygenic resistance in some plants of Wisconsin Hollander (4, 16). These genes appear to be cumulative for resistance. Crosses of susceptible varieties with those having polygenic resistance have considerably reduced resistance. Wisconsin All Seasons has both types of resistance. Apparently selection for resistance to yellows is effective in most varieties of cabbage (90, 137, 138, 246). These percentages of infected plants were found in Florida (45): Glory of Enkhuizen, 55; Resistant Detroit, 8.7; Resistant Premier, 7.3; Resistant Glory, 1.8; Resistant Medium Copenhagen, 0.

RESISTANCE TO INSECTS

APHIDS. It has been observed (22) that the varieties of cabbage with a flat head shape are more tolerant to the cabbage aphid, *Brevicoryne brassicae* L., than are those with round heads. Of those with round heads, the late varieties were less injured than the early and mid-season ones. In late summer the rate of reproduction of the aphid is correlated with the nitrogen content, especially the protein, of the host plant (47).

CABBAGE MAGGOT. European varieties of cabbage that are resistant to the cabbage maggot, *Hylemya brassicae* Bouché, in clude Erstling, Etampes, Express, Wiener and Zuckerhut (197). Charleston Wakefield and Early Jersey Wakefield had about 25

per cent less injury and 30 to 50 per cent more marketable heads under conditions of heavy field infestation than did Golden Acre and Super Curled Savoy (282). Penn State Ballhead also showed considerable resistance. The following year, under moderate conditions of infestation, the two Wakefields were 88 and 94 per cent free of injury compared with 47 and 12 per cent for Golden Acre and Super Curled Savoy, respectively (283).

IMPORTED CABBAGEWORM. The imported cabbageworm, *Pieris rapae* L., is attracted to plants containing glucosides of mustard oil (265). The effect of the wide difference between certain strains of Copenhagen Market and Volga on possible resistance to these insects might be worth investigating. The reported (72) tolerance of red cabbage to *P. rapae,* to the cabbage looper (*Autographa brassicae* Riley) and to the diamond-back moth (*Plutella maculipennis* Curt.) might have a similar basis.

RESISTANCE TO COLD

Resistance to cold depends upon the ability of a variety to harden at cool temperatures. Various factors may be involved, among which may be mentioned changes in protein during the hardening process which prevent it from precipitating at freezing temperatures (73). The presence of sugar is also an advantage, as it depresses the freezing point. Varieties with a high rate of assimilation and a high content of dry matter are said to be more resistant to cold (217). Such varieties have a low rate of respiration during thawing. Other theories have been advanced. Both Jersey and Charleston Wakefield are relatively hardy, as are some varieties of red cabbage (73). Copenhagen Market and its relatives are considerably less hardy than such varieties as Glory of Enkhuizen, Marion Market and Early Round Dutch at the U. S. Southeastern Vegetable Breeding Laboratory.

LINKAGE

The more striking cases of linkage involve crosses between botanical varieties of *B. oleracea.* In a cross between cabbage with entire leaves and a non-heading kale with curled leaves, no heading plant with curled leaves was obtained in the second or later generations, although several genes must have been involved for each pair of contrasting characters. As the quality of the head decreases, the degree of curling increases proportionately (3, 134, 183, 207).

In similar manner heading can not be combined with enlargement of the stem of kohlrabi (183). There seems to be no morphological reason why this might not occur. The same is true of heading in cabbage and the flower clusters of cauliflower (183), although normal buds may occur within the intact heads of cabbage lines that bolt readily.

It is perhaps to be expected that those plant characters typical of cabbage tend to remain together in crosses with non-heading forms. Two such groups have been observed (134, 183): (*a*) factors for heading and those for sessile, entire, and wide leaves; and (*b*) other genetic factors for heading and genes for short stems and non-curled leaves. Allgayer (3) proposes groups to include (*a*) factors for heading, color (*P*), petiole blade, leaf width, frilled leaves, and broad vs. narrow stem; and (*b*) other factors for heading, stem length, additional factors for leaf frilling, and probably a second factor for petiole blade.

Allgayer (3) found 20 per cent crossing over between his factors for heading, *K*, and for purple blade, *P*. Pease (183) considers the *D* factor for purple leaf independent of his recessive genes, n_1n_2, for heading. He obtained 10 per cent crossing over between the gene for petiolate leaf, *Pet*, and his N_1 for non-heading. There is 30 per cent crossing over between *T* (tall plant) and N_2.

Kristofferson (112) reports linkage between the color factors *B* and either *A* or *C*. Malinowski (134) indicates linkage between factors for enlargement of the stem in kohlrabi and the color gene *D*. Kwan (118) found 10 per cent crossing over between R_1 and *W* or R_2 and *Sm*.

The recessive factors for bolting are independent of genes for heading (43) and of the dominant factor for red (207). Different factors for heading are independent of each other, as are the different factors for frilling of the leaves (3). Both sets of factors are independent of genes for petiole blade, for the asparagodes leaf character and for axil sprouts (3, 183). A peculiar combination of enlarged axil buds within cabbage wrapper leaves is reported (8, 43, 134) and observed at the U. S. Southeastern Vegetable Breeding Laboratory. This indicates the possibility of a recombination of some of the genes distinguishing cabbage from brussels sprouts, although some linkage of genes within each group seems likely. No difficulty is experienced in combining factors for high

ascorbic acid with those for resistance to yellows (53, 271, 275). There is no way of distinguishing between complete independence and loose linkage in such instances. The color factor *D* is independent of the factors for heading (183).

LIST OF GENES

To avoid the confusion resulting from the use of the same symbol for different genes, slight changes are suggested for those symbols lacking priority. Because of the close genetic relationship among the botanical varieties of *B. oleracea,* the genes and their symbols for all of these crops can be regarded as belonging to a single group.

A—Basic color factor without effect alone (111).

As—Asparagoides. Bizarre protuberances from leaf midrib and veins; originally designated *A* (183).

Ax—Axil sprouts; originally *A* (3).

B—Light red midrib alone (111). With *A* gives a dark red violet.

Br—Broad stem; originally *B* (3).

B_1B_2—Major factors for the stem enlargement of kohlrabi (134).

B_3—Minor factor for the stem enlargement of kohlrabi (134).

C—Color factor, with *A* produces a dark-violet midrib (111, 134).

D—Color factor for purple leaves. Requires a complementary factor, perhaps *A* (111).

E—Color extending factor (111).

En—Entire vs. lyrate leaf; originally *E* (183).

G, H—Complementary factors for deep purple. *Gh*—sun color; *gH* and *gh*—green (118).

K—Dominant factor for heading (3).

k_1, k_2, k_3—Recessive factors for heading (3).

M—Magenta plant color (129).

n_1n_2—Recessive factors for heading (183). It is here suggested that these might be extended and substituted for Allgayer's k_1, k_2, k_3, etc. (3).

P—Purple blade when homozygous; purple veins when heterozygous (3).

Pet—Petiolate leaf vs. sessile; originally *P* (183).

R_1, R_2—Duplicate factors for sun color (118); need reconciling with *G* and *H* and also with *S*.

S—Sun color (129). See *G, H,* R_1, and R_2.

Sm—Recessive *sm* with recessive *wr* produces smooth leaves; originally *S* (118).

s_1, s_2, s_3—A series of incompatibility alleles (98, 171).

Sp_1, Sp_2, Sp_3 and Sq_1, Sq_2, Sq_3—Independent allelic series of incompatibility factors (143).

T—Tall vs. short plant (183). Designated *L* by Allgayer (3).

T_1, T_2, T_3—Allelic series of fertility factors (98).

W—Wide vs. narrower leaf (134, 183).

Wh—Dominant white flower; *wh*—yellow flower (177).

Wr—Recessive *wr* with recessive *sm* gives smooth leaves; originally *W* (118).

W_1, W_2, W_3, W_4—A series of factors for frilled leaves, each probably independent (3).

CYTOLOGY

The chromosomes of cabbage are relatively small. The genome of nine has been classified according to size (218). There are 1 very long, 4 long, 3 medium and 1 short chromosomes. Meiosis in the pollen mother cells appears to be normal through diakinesis (29). Some secondary association has been observed at early M I (29) and at M II (29, 68). The maximum secondary association is 3 groups of 2 bivalents plus 3 pairs c^c chromosomes. Studies of secondary association in this and other species of *Brassica* have led Sikka (218) to conclude that five is the basic chromosome number for the genus. He regards *B. oleracea* as a modified amphidiploid from a cross between two primitive 5-chromosome species, with subsequent loss of one pair of chromosomes. Catcheside (29) considers 6 to be the basic chromosome number for the genus. The haploid chromosomal complement of cabbage is thus considered to be AABBCCDEF (29, 68).

Pearson (181) found that the antipodal cells usually disappear before fertilization. The embryo does not begin to develop for at least four days after fertilization occurs. Growth of the embryo is slow at first, reaching the four-cell stage on the sixth day after fertilization. Cotyledons appear about the thirteenth day. The embryo fills the ovule about the thirty-second day after fertilization.

Tetraploid cabbage has been obtained through regeneration after decapitation (213) and by treatment with chemicals (167, 220). The tetraploid plants are said to be larger in all respects than the

diploid, except the size of the chloroplasts (167, 213), although size of head may sometimes be smaller in the tetraploid (214). There is some disagreement among these reports (167, 213). In the former paper (167), heads of the tetraploid are said to be somewhat larger and fertility unreduced as compared with those of diploid. In the latter (213) the tetraploid heads are smaller and the fertility about 70 per cent of the diploid. Most chromosomes are bivalent through diakinesis and M I (214); quadrivalents were also observed (167, 213).

An octoploid cabbage secured by decapitation of the tetraploid had larger deeper-yellow flowers than the tetraploid (214). Meiosis was irregular and the plant was nearly sterile, producing only three seeds under controlled pollination and only seven seeds when open-pollinated. No seed was obtained in crosses with either diploid or tetraploid.

Reitberger (199, 200) has made the interesting observation that the number of chromocenters in the very young resting nuclei of both diploid and tetraploid cabbage plants corresponds very closely to the somatic chromosome number of these plants. The chromocenters appear as dark-staining bodies, subspherical or elliptic in shape. Their size varies considerably but they are always smaller than the chromosomes.

B. oleracea L. var. *acephala* DC. Collards and Tree Kales

ORIGIN AND HISTORY

Collards and tree kales, together with their close relatives, the kitchen kales and thousand-headed kale, are among the oldest known members of the cole group (20). They appear to have originated in the Mediterranean area or in Asia Minor. Both collards and kales were grown and eaten by the Greeks and the early Romans well before the Christian era. Collards are widely grown for winter greens in the South. The tree kales are grown in England and in other parts of Europe, where they are often used as forage for livestock.

GENETICS

PLANT CHARACTERS. Most of the genes in collards and kale, or their alleles, have already been mentioned. They carry the partially dominant series of genes for non-heading. As the term

acephala implies, non-heading is the principal feature of this group. This is shared with the wild *B. oleracea* var. *sylvestris* and related species. Compared with those of cabbage, the leaves are narrower, because of recessive *ww*, and pointed. Pointed is dominant to the rounded or depressed apex of cabbage leaves (111). The leaves vary rather widely in shape. They are often lobed and have been described as lyrate, due to the recessive *en en*, as opposed to entire. The leaves are petiolate (*Pet Pet*) instead of sessile. Both collards and the tree kales have the dominant gene for tallness, *TT*. The thickened stem of narrow stem kale is a special modification of economic value. A dominant gene *Br* (originally *B*) (3) increases thickness of stem.

The basic color gene *A* has been found in green plants (111). Purple plants result from the same color genes as in cabbage. No report of sun color has been found.

DISEASE RESISTANCE. Kale is reported to be the source of genes for resistance to club root (273). Collards may have a high degree of resistance to the anthracnose leaf spot of crucifers (211). Kale is said to be immune from turnip mosaic (virus 1) (249).

B. oleracea L. var. *botrytis* L. Cauliflower and Cauliflower-broccoli

ORIGIN AND HISTORY

The flower bud curd of cauliflower represents an increased degree of specialization compared with flowering shoots of sprouting broccoli (8). Its appearance terminates the vegetative stage of the plant. Under favorable conditions some of the shoots grow out and produce normal flowers (35, 195). Cauliflower has a cultural history that goes back to the sixth century B.C. (20). It is native to Asia Minor and areas adjacent to the Mediterranean. Cauliflower and cauliflower-broccoli are similar in appearance. The latter is hardier and grows more slowly than cauliflower (20). Both are sold as cauliflower on the market.

GENETICS

The leaves are long and comparatively narrow (*w w*), petiolate (*Pet*) and lyrate or partially lobed (*en en*).

The distinguishing feature of cauliflower—the compact curd of immature flower buds—is partially dominant when cauliflower is crossed with kohlrabi, although the high quality of cauliflower is

lost (286). Somewhat similar results were secured from crosses with sprouting broccoli (286). The flowering heads of the F_1 plants are leafier than those of either parent. The cross between cauliflower and cabbage produces a long slender head having a heavy core and ten to 20 axillary heads inclosed (182, 286). This appears to be similar to the plant rarely found in cabbage that seems to combine genes from cabbage and brussels sprouts. However, the cross between cauliflower and brussels sprouts does not give plants with enlarged axillary buds (286).

Most varieties of cauliflower carry genes for resistance to cabbage yellows (198). The resistance of different varieties gave a range of 16.5 to 93.5 per cent of the plants affected in greenhouse test. The Pioneer variety is most resistant. Affected plants may outgrow the disease and mature normally. Cauliflower also is resistant to a mosaic disease of rape found in China (123).

CYTOLOGY

The *n* chromosome number of nine (100) has been doubled by application of colchicine to the growing point (234). The fertility of the tetraploid is reduced from 19 seeds per silique in the diploid to 12 seeds. Chromosome distribution at A I is normal.

B. oleracea L. var. *fimbriata* Mill. Kitchen Kale
B. oleracea L. var. *fruticosa* Metz. Thousand-headed Kale

All of the oleraceous kales are closely related botanically and may be said to have the same history. All have been cultivated in the Mediterranean area for at least 2000 years (20). Aside from their culinary value, the kitchen kales are of interest for their curled and finely divided or fimbriated leaves. This feature and their striking coloration provides the basis for the ornamental types. Segregation of leaf shape and heading in the cross with cabbage is explained by assuming three multiple genes, *ABC*, of equal value, for heading, and three multiple genes, *xyz*, for curliness, with complete or very close linkage between *A* and *x*, *B* and *y*, and *C* and *z* and their respective alleles (131). Cabbage is thus *AxAxByByCzCz* and kale is *aXaXbYbYcZcZ*. Segregation of complete heading with non-curled leaves through various combinations of reduced heading with an increased curliness of leaves to completely non-heading fully curled leaves followed a straight line. Kristof-

ferson (111) obtained a continuous variation for these characters in the F_2, but neither true parental form was recovered in a population of 14,000. The results of Pease (183) seem to be in close agreement with the original data of Malinoski (131). These genetic symbols have not been included in the list of genes because it is assumed they were meant to represent a generalized formula. There are both tall, *T*, and short, *tt*, varieties.

An examination of several varieties of kitchen kale by means of penetrometer and shearing tests indicate that Curled Siberian is more tender than Dwarf Blue Curled Scotch with respect to both mid-rib and blade (125). Long Season and Smooth kales were intermediate. An examination of the tensile strength of removed fibrovascular bundles and a palatability test both confirmed the rating.

The fertility of tetraploid thousand-headed kale is approximately half that of the diploid form. There are about four tetravalent chromosomes per cell. Chromosome counts at M II gave 58 per cent with 18 chromosomes and 20 per cent with 17 chromosomes. Plates with 16 and 20 chromosomes were also observed (80, 81). The tetraploid × diploid cross is successful but not the reciprocal. The average weights of seeds are $2x$—0.00408 gm., $4x$—0.00534 gm., and $3x$—0.00120 gm.

B. oleracea L. var. *gemmifera* Zenker. Brussels Sprouts

Brussels sprouts originated in northern Europe no more than 400 or 500 years ago (20). It is thus a relative novelty in the cole group. It takes its name from the Belgian city, in the vicinity of which it has long been grown. The enlarged axil buds are the character of economic importance.

In extensive crosses of brussels sprouts with broccoli, cabbage and kale, Kristofferson (111) identified the color genes *B*, *C* and *E* in this crop. The leaves are entire petiolate, *Ln Pet.* Plants carry the factor *T* for height.

Pease (183) points out that the genetic factors for heading and those responsible for the development of axillary buds are independent, but the two types are rarely found in the same plant in cultivated varieties. The cases reported (8, 43, 134) can hardly represent normal development for either type. The first generation of brussels sprouts × cabbage combines a long head with loose

lateral buds (286). In a cross between brussels sprouts and kohlrabi there was some development of axial buds in the F_1 (286). In the second generation there were 61 brussels sprouts, 8 plants with small lateral buds and 44 without axillary bud development. A 9:1:6 ratio is suggested. Both time and degree of development of the lateral buds varied. Brussels sprouts × broccoli F_1 plants have poorly developed lateral buds (286). The cross with cauliflower results in no axillary heads (286). The first generation of brussels sprouts × kale has leafy lateral buds. Several factors appear to be involved. They are somewhat different in each botanical variety.

The dominant gene for resistance to *Fusarium* wilt is present in certain plants (17). Brussels sprouts carry factors for resistance to anthracnose leaf spot, caused by *Colletotrichum higginsianum* Sacc. (211). Brussels sprouts are also highly resistant to turnip mosaic (virus 1) (249).

B. oleracea var. *gongylodes* L. Kohlrabi

Kohlrabi is sometimes placed in a separate species, *B. caulorapa* Pasq. (7, 10), but its breeding behavior with the botanical varieties of *B. oleracea* would seem to be sufficient basis for retaining kohlrabi as a botanical variety of *B. oleracea*. Kohlrabi is thought by some to have been developed in northern Europe in the 15th century (20) and by others to be one of the oldest varieties of *B. oleracea* (184). The difference of opinion apparently turns on whether the description of a cole by Pliny referred to kohlrabi or to cauliflower. Americans apparently have never adopted a vernacular term for the specialized enlargement of the stem characteristic of kohlrabi. Bailey (10) uses the botanically correct " tuber ". The British have adopted the highly descriptive " bulb ", which will be used here for convenience with the understanding that the term refers to shape rather than structure.

When kohlrabi is crossed with any other variety of *B. oleracea*, the size of the bulb is intermediate (184, 286), and the epidermal layer is coarse and hard as in kale or cabbage (184). In the second generation of crosses with cabbage and kale, there is wide variation. Some bulbs attain the size of the kohlrabi parent but lack its quality. There were 312 bulbed; 4472 intermediate; and 78 plants without a bulb. If two major factors, B_1 and B_2, and

one minor factor, B_3, are assumed, the expected numbers would be 304:4482:76. The backcross to cabbage gave 545 intermediate to 81 non-bulbed (7:1), and to kohlrabi gave 87 bulbed to 251 intermediate (1:3). The third generation gave added support to the 3-factor hypothesis (184). Malinowski (132) obtained no well-developed bulb in the second generation. Yeager (286) reports a coarse heavy stem and various degrees of branching in crosses between kohlrabi and the other forms. This may result from hybrid vigor.

The two principal varieties are White Vienna and Purple Vienna. The purple color has a two-factor basis. The leaves are petiolate *Pet,* entire *En,* and broad *W.* All three are linked to one of the factors for bulbing, and perhaps also to the color factor *D* (184). The dominant gene for resistance to *Fusarium* wilt has been found in kohlrabi (17). An antifungal substance has been detected in the epidermis of kohlrabi, effective against the wilt organism, that may account for its resistance (64). Kohlrabi is highly resistant to the anthracnose leaf spot of crucifers (211). It also carries genes for resistance to a mosaic of rape and other crucifers (123) and to turnip mosaic (virus 1) (249).

Progress is reported (115) in the development of cold-hardy lines through selection. They are also non-woody.

B. oleracea L. var. *italica* Plenck. Sprouting Broccoli

This Mediterranean plant is another of the older oleraceous vegetables (20). Sprouting broccoli is distinguished from cauliflower-broccoli by having a looser cluster of flower buds on longer stems and several lateral branches terminating in smaller clusters of buds. It takes part of its name from these lateral shoots or " sprouts ".

The second generation of cabbage × broccoli is more variable than the second generation of cabbage × kale, apparently because of greater differences in genes for type of leaf in the former cross (111). No true broccoli was recovered in a population of 279 plants. A 3:1 ratio for red color was obtained. This is in spite of the genetic formulae suggested for the two (red cabbage—*DDAAbbccee* and broccoli—*ddaabbCCEE*). Perhaps the broccoli employed in the reported cross was *ddAAbbCCee.* In this case it would have a deep-purple mid-rib, but a green leaf blade.

Broccoli, like cabbage, has genetic factors for incompatibility. The number of seeds obtained per pod varies with the material. In one case (180) incompatible matings gave 1.0 to 2.7 seeds per pod; compatible matings, 3.8 to 6.9 seeds; and open pollination, 3.0 to 9.7 seeds per pod. In another instance (212) incompatible matings of self- and cross-pollinations gave 2.5 and 3.7 seeds per pod, while compatible matings yielded 18.2 seeds per pod. Germination of pollen decreased from 92.8 per cent in compatible pollinations to 39.4 per cent where the cross was incompatible. In the latter case cytoplasm ordinarily does not enter the tube, which is no longer than the diameter of the pollen (212). Pollen germinated 85.5 per cent after bud pollination of incompatible matings. The stigmatic layer contains the inhibiting material, since normal fertility results from its removal. Self-compatible plants may segregate from the bud pollination of self-incompatible plants. Reciprocals do not always give the same results. Sears (212) doubts the existence of a factor stimulating the growth of pollen tubes proposed by Kakizaki (98). Work with tetraploid broccoli indicates that certain plants frequently differ in compatibility in reciprocal crosses (15).

MUSTARD GROUP

B. nigra (L.) Koch. Black Mustard

Black mustard has eight pairs of chromosomes, the lowest number of the *Brassica* species (218). It is cultivated to some extent in Europe as a source of table mustard (10, 160), but has become an important weed in North America. Black mustard was first described as *Sinapis nigra* L.; later it was transferred to *Brassica*. It is more compatible with the European than with the oriental species of the genus. Its unique relationship to *B. carinata* A. Br. and to *B. juncea* (L.) Coss. will be described later. There are two major geographic forms, eastern and western (222). The western form is grown in Europe, Africa, Asia Minor and Afghanistan. The eastern form is grown in India and as far west as Palestine and Syria.

There are eight pairs of chromosomes at diakinesis, two pairs being attached to nucleoli (218). An occasional tetravalent chromosome was observed. There is sometimes a high degree of secondary pairing at M I. This usually involves two pairs, but

sometimes more. It is suggested that *B. nigra* may be an allotetraploid resulting from a cross between two unrelated primitive 5-chromosome species with later doubling of the chromosomes and the loss of two pairs of small chromosomes (218). There are 4 satellites, 4 nucleoli, and 2 very long, 8 long, 6 medium and 0 small chromosomes. The haploid set is AABBCCDE (218). Secondary association, giving two groups of 4 chromosomes each, plus 4 pairs, has been observed by Haga (68). This worker regards the genome as ABCDEEFF. Crosses between diploid and tetraploid forms are reciprocally unsuccessful (83).

B. chinensis Jusl. Pak-choi, Chinese Mustard

Pak-choi is known both as "Chinese mustard" and as "celery mustard". It is one of the rather numerous 10-chromosome oriental species of the mustard group. It is a smooth-leaved non-heading annual (228) or biennial (8). The leaf stalks are light in color. The tap root may become enlarged in cool moist soil (7). The leaves are broad as compared with those of *B. parachinensis* Bailey (10).

The cross between the non-heading Pak-choi and the head-forming Pe-tsai gives non-heading rosette plants in the first generation (226).

There are three types of sterility or incompatibility: (*a*) abscission of flowers at the beginning and at the end of the blooming period, (*b*) proliferation of pistils, preventing their normal functioning, and (*c*) physiological incompatibility of plants with normal flowers. Self-compatible plants are most productive of seed in mid-bloom. Such plants may be self-incompatible earlier or later in the blooming period (226). Fertility is improved by bud pollination (122).

The somatic chromosomes are placed in six morphological groups (202). This gives the following chromosomal formula: ABCDDEEFFF. The location of the constriction and the range in length (microns) are given for each morphological type: A—sub-median 2.9 to 3.1; B—nearly median 2.2 to 2.5; C—sub-terminal 2.0 to 2.3; D—sub-median 2.0 to 2.5; E—sub-terminal 1.1 to 1.4; and F—median or sub-median 0.7 to 0.9.

Regular pairing results in ten bivalents at diakinesis and first metaphase (202, 216, 284). Secondary pairing of up to four

bivalents is reported (202, 284). The association of two pairs is most common. Secondary pairing may be between long and short chromosomes (202). Two chiasmata are most common. Size differences observed in the somatic chromosomes are apparent at M I in that five large and five small pairs can often be distinguished. In spite of the six morphological types described, four is considered to be a possible primitive basic chromosome number in *B. chinensis* (202). The number four is based on the maximum number of groups found in secondary association. The association of morphologically unlike pairs "suggests that possibly the chromosomes . . . have been in some way structurally rearranged". At the same time it is pointed out that structural hybridity might affect secondary pairing and thus weaken the supposition of a basic number of four (202).

In addition to normal bivalent pairing, univalents, trivalents and quadrivalents occur in the tetraploid (284). Frequency of quadrivalents was observed to be 3.28 per PMC. Secondary association occurs frequently. Univalents lag at A I. Second metaphase plates have 17 to 22 chromosomes. Secondary association is also observed at M II. The proportion of apparently good $2x$ pollen is high—72.6 to 93.8 per cent. The diploid has 94 to 98.3 per cent of good pollen. The tetraploid has fewer viable seeds per pod (1.41 to 4.3) than the diploid (6.6 to 6.8).

B. pekinensis (Lour.) Rupr. Pe-tsai, Chinese Cabbage

Pe-tsai is another of the 10-chromosome oriental species of the mustard group. Chinese or celery cabbage has rather loose heads, often a long, narrow cylinder, or sometimes broadly oval. The genes for heading are recessive in crosses with Pak-choi (226). The leaves are yellowish green, without bloom, nearly glabrous, long and comparatively narrow, and of a soft texture compared with those of common cabbage. The mid-rib is wide and light in color.

Individual plants differ widely in their degree of self-incompatibility (94). Some plants produced 1215 seeds per 100 open-pollinated flowers and only 159 seeds per 100 flowers when self-pollinated (95). The following data are in terms of per cent of the pod set after open pollination: bagged unpollinated, 4.8; self-pollinated, 30.3; pollen from another flower of same plant, 23.4 to

35.3; pollen from another plant, 96.0 (94). As in *B. chinensis,* early and late flowers may abscise and the pistil may be sterile because of proliferation (226). Cyclic incompatibility was also observed wherein fertility was greatest during mid-bloom. Complete incompatibility involves coiling of the tubes and limited pollen tube growth (227). The degree of self-compatibility was increased by selection but it never reached 100 per cent. Bud pollination increases the seed production of self-incompatible plants. The increase was from 0.13 to 17.6 seeds per flower (99). In other work bud pollination increased the per cent of pods set from 15.9 to 74.3 (122). A dominant gene for self-fertility in crosses with *B. rapa* L. has been reported (23).

The somatic chromosomes are morphologically similar to those of *B. chinensis* except that the C and D types are a little shorter and the E and F types are a little longer in *B. pekinensis* (202). The formula for the genome is the same—ABCDDEEFFF. The length of both E and F chromosomes is the same as for *B. rapa.* Meiosis is regular (210), with ten pairs at diakinesis (202). Two chiasmata are most common. Secondary association most commonly involves two pairs, but may include four pairs, some of which may differ in size (202). In the cross between *B. pekinensis* and *B. chinensis* there is a maximum secondary association of five pairs of chromosomes. Richharia (202) concludes that there is a possibility of a primitive basic number of five for *B. pekinensis.*

B. campestris L. var. *annua* Reichenb.	Summer Turnip-rape
B. campestris L. var. *autumnalis* DC.	Winter Turnip-rape

Brassica campestris L. extends naturally from the British Isles, across Europe and northern Africa, and on across Asia south of the 45th parallel and north of the Himalayas through nearly all of China to the middle of Korea (222). It is a highly polymorphic species, to which numerous brassicas have been referred at one time or another. Olsson (175) considers all of the 10-chromosome species listed in Table I to be subspecies of *B. campestris.* The species is common as a weed in Europe (wild rape) and in North America (field mustard). The turnip is said to have originated from *B. campestris* (92). Some still refer the turnip to this species (160, 222). As in *B. napus,* with which it has some characteristics in common, there are annual and biennial forms. Neither

botanical variety is grown commercially in the United States, but seed is imported for oil and for bird feed (160).

The *campestris* genome is made up of 1 very long chromosome, 4 long, 3 medium, 1 short and 1 very short chromosomes. Each cell has 2 satellites and 2 nucleoli (218). Meiosis is regular (216). In toria (*B. campestria* var. *toria* Prain) there are ten pairs of chromosomes at diakinesis and M I. Each M II plate has ten chromosomes (194). Triploid toria commonly has eight trivalents, two bivalents and two univalents at M I. The univalents are outside the plate. They are usually included, undivided, in the daughter nuclei (194).

B. rapa L. Turnip

ORIGIN AND GEOGRAPHIC DISTRIBUTION

There are two major geographic groups of turnips, western European and Asiatic, and four minor groups—Russian, Asia Minor, Afghan-Indian and Japanese. Each of these groups can be characterized by the type of its lower leaves, while other characters, such as color and shape of the root, may vary widely (222). The Afghan-Indian, Japanese and European groups have forms with entire and with dissected leaves. The evolution of the turnip from the wild *B. campestris* is said to have been through the annual and the biennial forms, finally to the turnip (92).

GENETICS

SHAPE OF ROOT. After extensive study of the different geographic forms, Sinskaia (222) proposes 12 root shapes as follows: (*a*) long spindle, (*b*) long cylindrical, (*c*) long, broad below, (*d*) long horn, (*e*) semi-long, beet-root, (*f*) semi-long, broad below, (*g*) top, (*h*) orbiculate, (*i*) flat-orbiculate, (*j*) orbiculate-flat, (*k*) Milan flat, and (*l*) Retrovsky flat. Evolution of the root has been from long thin to short flat. A cross between round and long gave an intermediate F_1 and 1 long to 14 intermediate to 1 round in the next generation (91). Two genes are proposed, $L_1L_1L_2L_2$ for long and $l_1l_1l_2l_2$ for round. Intermediate × short give intermediate, which segregate long and intermediate. Two multiple factors could also explain this segregation. Other crosses, such as between long and "longish", yielded long to short, conical and spherical in the second generation (92). Several genes must be assumed to ac-

count for these types. The 12 classes for root shape mentioned indicate that a rather large total number of genetic factors are probably concerned with shape of root.

FLESH COLOR. The dominant gene *M* gives a white interior root color. The recessive *m* results in yellow flesh. These genes also govern flower color: *M* citron yellow and *m* light orange (36, 91). There are no yellow-fleshed turnips in Asia (222).

EXTERIOR ROOT COLOR. Cultivated turnips of the European group have a violet-red, green or yellow top and a faint orange-yellow or whitish lower portion. The three colors of the upper portion of the root are controlled by three factors: *M* reduces the intensity of yellow, which is expressed with *mm*; *V* is responsible for green; *P* gives violet red and is epistatic to *V* (91). Plants heterozygous for *P* and heterozygous for *V* are lighter in color than when homozygous dominant (92). The various combinations are as follows:

Genotype	Top exterior	Interior	Corolla
PVM	Whitish violet-red	White	Citron yellow
PVm	Yellowish violet-red	Yellow	Light orange
PvM	Whitish violet-red	White	Citron yellow
Pvm	Yellowish violet-red	Yellow	Light orange
pVM	Whitish green	White	Citron yellow
pVm	Yellowish green	Yellow	Light orange
pvM	Cream yellow	White	Citron yellow
pvm	Deeper yellow	Yellow	Light orange

Davey (36) crossed red and green and got a purple first generation and 9 purple : 3 red : 3 green : 1 white in the second. Sinskaia (222) distinguishes red and purple and also includes white and black or gray. No genetic study of these colors is reported.

EPIDERMAL CHECKING. There is a coarse checking or breaking of the epidermis that is inherited. A cross between broken epidermis and normal gives plants that are intermediate and that segregate in the second generation. Certain crosses between normal produce a normal F_1 but a segregating F_2 (92). This suggests the possibility of two factors. The cracked rind is said to bear a resemblance to alligator skin.

FLOWER ABNORMALITY. A self-fertile apetalous plant found in a field of lucerne proved to breed true for this character (193). The reciprocal crosses with normal turnip produced normal flowers. A second generation was not reported.

BOLTING. There are wide varietal and strain differences in the tendency to bolt (279). Percentages of bolting plants in Virginia sown March 20 and harvested June 6, 1935 were: Shogoin, 100; Seven Top, 35 to 52; White Milan, 8 to 38; Purple Top White Globe, 0 to 17; White Flat Dutch, 2 to 9; Snowball, 0 to 2; and four European varieties, 0. Golden Ball had not flowered on July 3. Purple Top Strap Leaf had two per cent on each date. Golden Ball and Shogoin again represented the extremes in 1936. All but Shogoin reached prime market before flowering. Later planting reduces the proportion of plants bolting.

DISEASE RESISTANCE. Several varieties of turnip are known to be highly resistant to club root, or finger and toe, caused by *Plasmodiophora brassicae* Wor. The Bruce variety, grown for many years in Aberdeenshire, Scotland, was one of the first to be recognized as resistant (50, 74). It apparently carries *PVm*. Other varieties highly resistant in greenhouse tests are Immuna, Golden Ball, May, Purple Top Milan, Rhode Island Rock, Snowball and Yellow Aberdeen (270). In the same tests Shogoin had 83 to 97.6 per cent infected plants. Another highly resistant variety, Immuna II, was later reported (119). Two crosses between resistant and susceptible gave the following F_2 segregation: 1036 healthy, 462 slightly diseased and 312 heavily diseased (57.2:25.6:17.2), and 960 healthy, 420 slightly diseased and 353 heavily diseased (55.4:24.2:20.4) (243). Resistance is considered to be due to multiple factors. No linkage was found between genes for resistance and genes for color, but there may be linkage between factors for resistance and for length of root.

A substance called "rapine" that is highly toxic to *Fusarium oxysporum* has been found in epidermal cell layers of the root (64). It is obtained by steam distillation and can be extracted with ether. It is a good fungicide at dilutions up to 10^5, but is not a bactericide.

White Milan is very susceptible to four mosaic viruses of turnip, T_1, T_6, T_8, and T_9 (121). Purple Top White Globe is somewhat tolerant.

INSECT RESISTANCE. Fairchild (48) makes brief mention of the Petrosky variety of turnip resistant to the turnip root maggot. The variety has long been grown in Finland. The Shogoin variety has resistance to aphids (206).

CYTOLOGY

The somatic chromosomes fall into the same six morphological groups described for *B. chinensis*. The A, E and F chromosomes are a little longer in the turnip in which there are three E's instead of two and two type F instead of three. The genome is then ABCDDEEEFF. The type of constriction in type E is submedian or median instead of sub-terminal as in *B. chinensis* (202). Catcheside (28) makes four groups of the somatic chromosomes. In terms of microns, one chromosome is 0.5, one with median constriction is 2.0, five having a median constriction are 1.0 to 1.8, and three of the same length have a subterminal constriction. The shortest measurement (0.5) is considerably below the shortest (0.9 to 1.2) noted by Richharia (202), and the longest (1.0 to 1.8) is also below his longest (3.3 to 3.6 microns). Haga's chromosomal formula is AABBCCDDEF (68).

Both authors (28, 202) find ten pairs of chromosomes at diakinesis. Both also observe later secondary association, four being the maximum number of groups and three most common. Catcheside (28) proposes structural hybridity for four chromosomes, resulting in the following somatic formula: AAAAcBBBBfCCCCDDDDEEEaEb. Neither univalents nor quadrivalents were observed.

Both direct and reciprocal crosses between diploid and tetraploid forms are unsuccessful (83).

B. juncea (L.) Coss. Leaf Mustard

B. juncea is one of the polymorphic Asiatic species of *Brassica*. According to Bailey (8), " Its disguises are so many that one often has difficulty in finding characters common to all forms. This is true even of wild plants, although naturally in less degree ". Vavilov (264) gives central Asia (northwest India, including Punjab and Kashmir) as the primary center of origin, and lists three secondary centers: (*a*) central and western China, (*b*) the Hindustan area—eastern India and Burma, and (*c*) Asia Minor through Iran. Common names other than leaf mustard include brown mustard, Chinese mustard and Indian mustard or raya.

Incompatibility exists in certain forms (95). One hundred protected flowers yielded 49 seeds, while 100 open-pollinated flowers produced 1002 seds. Other forms are fully self-fertile (1).

Leaf mustard carries resistance to a mosaic disease of Chinese

cabbage that also attacks cabbage, cauliflower, rape, turnip and radish (251). Leaf mustard and white mustard appear to be the only brassicas with marked resistance to the disease. Southern Giant Curled is highly resistant to anthracnose leaf-spot, caused by *Colletotrichum higginsianum* Sacc. (211).

Indian mustard has shorter somatic chromosomes than other forms (2). The constriction is usually median. There are 18 pairs at diakinesis (68). Secondary association occurs at both first and second metaphase (2, 68). Maximum association gives four groups of four pairs each plus two pairs, making a total of six groups. There is no physical connection between any two pairs (2). Groups of three pairs have also been observed (68). This latter situation suggests the following haploid chromosomal formula: Aa,Aa,Ab,Ba,Ba,Bb,Ca,Ca,Cb,Da,Da,Db,Ea,Eb,Eb,Fa,Fb,Fb.

RAPE GROUP

B. napus L. Rape or Swede-rape and Rape-kale

B. napus is a Mediterranean species (264). There are annual and biennial forms. The rape-kales make up a third botanical variety (Table I). Some authors (160) include the rutabaga with this species. Others prefer to retain the distinction (10, 82). The annual form is planted extensively in Europe as an oil seed crop. The biennial form serves as a forage crop in this country (160). The rape-kales are also grown in Europe as forage. Musil (160) regards Siberian kale as belonging to this group. A chromosome count should serve to determine whether any individual plant belongs here or with *B. oleracea* var. *fimbriata*, the *B. fimbriata* of Bailey (9). It seems likely that there might be similar forms belonging to each species. *B. napella* Chaix, judging from the results of its cross with *napus*, is an oriental variety of *B. napus* (174).

The chromosomal formula for the genome proposed by Haga (68), AAAABBBBCCCCDDEEFF, while incomplete, does account for the cases of duplicate factors observed. For example (70), crosses between types with entire and with lobed leaves have small lobes at the base and along the petiole in the first generation, and give 15 lobed to 1 entire in the second generation (7803 to 493). The genes are E_1 and E_2. The four flower colors, together with the suggested genotype for each, are lemon-yellow—*AABB*, orange—*AAbb*, pale yellow—*aaBB*, and pale orange—*aabb* (233). While classification is somewhat difficult, 3:1 ratios occur in the

second generation of crosses between lemon-yellow and orange, and between lemon yellow and pale yellow. A haploid plant of *B. napus* var. *napella* had up to seven pairs of chromosomes at M I (155). In view of Haga's chromosomal formula (68), one might expect to find a larger number of bivalent chromosomes and perhaps a few quadrivalents.

The variety Club Root Resistant is, as its name implies, resistant to club root, although not immune (124). It is a fodder variety. Broad Leaf Essex and Giant types are susceptible.

Attempts to cross the diploid and tetraploid forms reciprocally were unsuccessful (83). Normal plants were observed to have 18 pairs of chromosomes at first division (156). It is assumed that this is an error, for 57 is given as the $3x$ number. Three triploid plants were somewhat dwarfed but had thicker stems and leaves. Univalent, bivalent and trivalent chromosomes were observed during the first division. There were 26 to 30 chromosomes on M II plates. One plant was a "dwarf gigas type with thick leaves and stems, and flowers slightly larger than normal" (156). This was assumed to be tetraploid. Pollen varied in size but few were empty. There were as many as five lagging chromosomes at A I. The numbers of good seeds per pod were $2x$, 13.5; $3x$, 3.9; and $4x$, 0.5.

Malinowski (133) crossed the biennial and annual forms. The second generation segregated 349 biennial to 57 annual. This segregation suggests that several factors are involved.

B. napobrassica (L.) Mill. Rutabaga, or Swede

The rutabaga, or swede as it is called in Europe, shares a striking parallelism with the turnip (264). Both have fleshy roots that are white or yellow within and have a similar exterior color series. Both have entire or lobed leaves. Both are closely related to a second species with slender roots, having annual and biennial forms, which is considered to be an ancestral form. It will be seen in the account of interspecific crosses in *Brassica* that this parallelism is by no means accidental but goes back to the probable origin of *B. napus*.

GENETICS

FLESH COLOR. The white- and yellow-fleshed forms were at one time placed in separate species (82). The cross (white flesh) Blanc hâtif à feuille entière × (yellow flesh) Bangholm gave 43

plants with white flesh. Both 3:1 and 15:1 ratios were obtained in the second generation (1046 white to 284 yellow and 1686 white to 87 yellow). The two factors are designated M_1 and M_2 (69).

EXTERIOR ROOT COLOR. As in the turnip, the exterior colors on the lower and upper portions of the root are distinct. In addition, there is a neck that may be of a color different from the upper portion. The lower part is faint orange yellow or whitish, and the upper portion is violet, green or intermediate. When the upper part is violet the neck is violet-red; when it is greenish red the neck is green. Thre are three types: red with reddish neck, red with green neck, and green with green neck. There are two dominant factors for anthocyanin: P_1 produces a faint red and P_2 a deep violet red, while p_1 and p_2 result in green (91, 92). Green × green gives all green without later segregation. Segregation from a red-green cross gives a 12:3:1 ratio (1087 deep violet red to 165 faint red to 31 green, and 3472 deep violet red to 728 faint red to 108 green). Heterozygous reddish green segregated 117 faint red to 19 green. The deficiency of green in each case is not accounted for. Results of later crosses (92), calculated on a percentage basis, suggest that the situation might be somewhat more complex than the two factor basis proposed. Davey (37) later points out that colors are affected by the environment and are difficult to classify. He proposes similar dominant genes N_1 and N_2 for anthocyanin on the neck and upper portion of the root. A cross between $N_1N_1n_2n_2$ and $n_1n_1N_2N_2$ segregated 15 purple to 1 green in the second generation.

Hallqvist (69) also reports a 12:3:1 ratio for the cross Bangholm (red) × Trondhjem (green). He crossed Bortfelder (yellow) × Ostersundom (red) and got various proportions of red, reddish-yellow and yellow to green in the second generation, depending upon the F_1 plant used. Red and reddish-yellow F_1 plants segregated all three types. One reddish-yellow segregated 81 red to 30 yellow-green; another segregated 74 reddish-yellow to 219 yellow-green. A yellow-green segregated 14 reddish-yellow to 144 yellow-green. Apparently the reddish-yellow plants are a modified yellow-green. Segregation in the third generation bears this out. Color of the petiole base follows that of the neck (107).

Flower colors and their inheritance are the same as described for *B. napus* (233). The same is true of leaf shape (70).

ASCORBIC ACID CONTENT. Varietal differences have been found in the ascorbic acid content of rutabaga. Varietal averages were 40 to 66 mgm. per 100 gm. in Minnesota (170). Golden Table Turnip had the least and New Yellow Garden the largest amount of ascorbic acid. Environmental differences were also important.

DISEASE RESISTANCE. Strains of rutabaga resistant to club root (finger and toe), caused by *Plasmodiophora brassicae* Wor., have been selected from susceptible varieties (281). Danish strains are said to have superior resistance (39). The Wilhelmsberg, Herning and Studsgaard strains of the Bangholm variety are highly resistant (39, 269). Most American varieties are resistant in this country, but are susceptible in Europe (44). There are two partially dominant genes for resistance and two partially dominant genes for susceptibility (225). No indication of linkage has been found between these genetic factors and the genes responsible for flesh color.

The Danish strains resistant to club root are also comparatively resistant to mildew, caused by *Peronospora parasitica* (Pers. ex Fr.) Fr. (39). Rutabaga is immune from a mosaic disease of the radish, to which most other brassicas are susceptible (250).

The variety Wilhelmsberger is said by some (40) to be resistant to the Swede midge (*Contarinia nasturtii* Kieffer), while others (39) think that this variety is "most susceptible". The "many necked" condition is largely the result of feeding on the shoulder of the root by this midge (40).

CYTOLOGY

The somatic chromosome count for both *B. napus* and *B. napobrassica* was for sometime thought to be 36 (28, 55). Further, the first generation of a cross between *B. napus* and *B. campestris* ($n = 10$) was $2n = 28$ "which just was the expected number", if the egg contributed 18 chromosomes and the pollen 10 (55). This appears to be a good example of finding what is expected by excellent investigators working with fairly difficult material. They considered *B. napus* to be a natural polyploid of 9-chromosome species. Once the situation was established to be the natural amphidiploid of a cross between a 9- and a 10-chromosome species, no one has challenged the chromosome number of 38. Credit must be given Nagai and Sasoaka (162) for reporting this number

before the true situation was established (78). In spite of the inaccurate count reported by Catcheside (28), his comparison showing similarities between the somatic chromosomes of rutabaga and turnip represents a step in the right direction.

There are 5 to 8 rod and 11 to 13 ring bivalents, but not all the chromosomes are in pairs at diakinesis. Chiasmata terminalize fully. A variable amount of secondary pairing was observed at M I (28). This may persist until second division. The secondary association is between pairs of equal size and with a similar number of chiasmata. On the basis of secondary association and the erroneous count of $2n = 36$, the following haploid chromosomal formula is proposed: AAAABBBBCCCCDDEEFF (28). The few univalent chromosomes observed at M I are explained as a failure of terminalized chiasmata to hold. A few multivalents may result from structural changes in the chromosomes. First anaphase is normal.

INTERSPECIFIC CROSSES IN BRASSICA

Crosses Between Species Having Similar Genomes

9-CHROMOSOME SPECIES—THE "C" GENOME

B. OLERACEA–B. ALBOGLABRA AND B. CRETICA. Both crosses are readily made, even between the Mediterranean *B. oleracea* and the oriental *B. alboglabra* (221, 222). The cross produced 12 seeds per pod, 100 per cent viable (221). The results support the essential identity of the c-genome when found in distinct but related species.

10-CHROMOSOME SPECIES—THE "A" GENOME

B. CAMPESTRIS–B. RAPA. Both sarson and toria cross readily with turnip (145). Davey (38) considers the turnip-rapes to belong to *B. rapa*, not to *B. campestris*. He may refer to these when he says that the cultivated forms of *B. rapa* are compatible with the wild *B. campestris*. There seems to be no question of the compatibility of the two species. Some workers prefer to identify the turnip as *B. campestris* var. *rapa* (L.) Hartm. (161) or var. *rapifera* Metzg. (222).

B. CAMPESTRIS–ORIENTAL SPECIES. *B. campestris* crosses readily with *B. parachinensis* (221), and with *B. chinensis* and *B. pekinensis* (175, 221). *B. campestris* and Pak-choi cross spontaneously.

The fertile vigorous F_1 plants are nearer to *campestris*. Transgressive segregation was observed in the second generation. For example, some plants like Pak-choi were pubescent. A "considerable" number of F_2 plants were sterile (221). This may be the result of factors for incompatibility. The cross with *pekinensis* is readily made (175, 221). The first generation is intermediate and fertile. The second generation is both fertile and highly variable, but exhibits less diversity than the cross with *chinensis*. Sinskaia (221) considers *campestris* to be genetically nearer to *chinensis* than to *pekinensis*. Sarson crosses somewhat less readily with both *chinensis* and *pekinensis* than does *campestris* var. *annua* (175, 176). Nine flowers of *campestris* × *pekinensis* set 100 per cent and averaged 16 seeds per pod, and three flowers of *campestris* × *chinensis* set 77 per cent and averaged seven seeds per pod (176). The cross *chinensis* × *sarson* had seven of 63 M II plates with nine chromosomes (175).

B. RAPA–ORIENTAL SPECIES. White turnip × Pe-tsai and its reciprocal are easy to make (192). The first generation is vigorous and highly fertile, and has a slender root and lobed leaves. Both enlarged root and entire leaves are recovered in the second generation in simple mendelian ratio. Shape of the root, like that of the root of horse-radish, varies from round to very long. Some "bulbous" or thick-rooted plants had entire leaves. Other plants with enlarged root tended to form a head like Chinese cabbage. Both heads and roots were tender and of good flavor (192). *B. rapa* is also interfertile with *B. chinensis* but does not cross as readily with *B. japonica* as with the other two oriental species just discussed (23). Fertility in crosses of *B. rapa* with *B. chinensis* and *B. pekinensis* is considered to be due to three dominate genes, two of which are carried by *rapa*, while both Chinese species have the other one (23). Twenty-one flowers of Pak-choi pollinated with Red-top White Globe turnip gave 62 per cent set, which averaged 0.3 seed per pod (176). It appears from this that results depend to some extent upon the variety of each species used and might also be influenced by environmental conditions.

CROSSES BETWEEN ORIENTAL SPECIES. *Brassica chinensis* and *B. japonica* have fairly good interfertility (95). *B. pekinensis* and *B. chinensis* are said to be fairly interfertile (23), but Pe-tsai and "Chinese mustard", supposedly in this case *B. chinensis*, are re-

ported to be intersterile (95). In contrast, Olsson (175) finds the cross easy to make, and Pearson (176) obtained from 12 flowers of Wong Bok (*pekinensis*) pollinated with chinensis, 12 pods averaging 12 seeds per pod. Here again variety and environment as well as age of plant and the number of flowers pollinated may have influenced the results. *B. parachinensis* Bailey, Mock Pak-choi, and *B. nipposinica* Bailey are readily crossed (221). Eight flowers produced eight pods averaging 15.6 seeds per pod, all of which germinated. The parents cross naturally. Both first and second generations are completely fertile. Similar results were obtained with *B. chinensis* and *B. nipposinica* (175, 221), and with *pekinensis* and *nipposinica* (175).

B. RAPA–B. TRILOCULARIS (ROXB.) HOOK. F. & THOMS. Forty flowers of *B. rapa* × *B. trilocularis* produced 34 pods averaging 5.2 seeds per pod. All germinated (218). The first generation exhibited hybrid vigor. There were ten bivalents at diakinesis and M I. Non-disjunction of one pair was observed in five per cent of the PMC. Otherwise meiosis was normal. The F_1 plants were highly fertile in open pollination.

19-CHROMOSOME SPECIES—"AC" GENOMES

B. NAPUS–B. NAPOBRASSICA. Chopinet (31) reports that the cross is fertile. Results with the different forms of each species have varied somewhat. Broad Leaved Essex rape × rutabaga (swede) averaged 16.1 seeds per pod (25) and the reciprocal averaged 20.9 seeds. Giant rape × swede gave 11.1 seeds per pod and the reciprocal 19.3. Asparagus and Ragged Jack kales are quite compatible with rutabaga, and Fillgap kale crosses naturally with swede (38). One of the earlier reports, by Sutton (231), states that the F_1's of yellow-fleshed Tankard swede with Asparagus and Ragged Jack kales are sterile, but the cross between white-fleshed swede and Ragged Jack kale is fertile. There are 19 pairs of chromosomes at meiosis, which is entirely normal (210).

Crosses Between Species Having Unlike Genomes

8- AND 9-CHROMOSOME SPECIES AND THEIR AMPHIDIPLOID

B. NIGRA–B. KABER. This cross is reported as *B. nigra* × *Sinapis arvensis* L. (141). For this reason "s" is assigned to the *kaber* genome. The somatic chromosome number of the first generation

is 17. From 1 to 8 bivalents plus 15 to 1 univalents occur in PMC. Artificial doubling of the chromosomes gave one plant with $2n = 34$. There were 0 to 7 quadrivalents plus 17 to 3 bivalents and 0 univalents (142). Tetraploid black mustard × tetraploid charlock resulted in a relatively fertile hybrid (256).

B. NIGRA–B. OLERACEA. The first attempt to cross *B. oleracea* × *B. nigra* resulted in failure (95). It was later successful (141), giving 27 plants with 17 somatic chromosomes. Four bivalents represent the maximum pairing. There may be 9 to 17 univalents. One plant was obtained from *B. nigra* × triploid *B. oleracea.* It had 26 chromosomes—acc genomes (8+9+9). The nine chromosomes of each c genome pair, leaving eight univalents of the a genome. The amphidiploid of the *oleracea–nigra* cross has 34 somatic chromosomes (142). During meiosis there are 0 to 4 quadrivalents and 17 to 9 bivalents. The amphidiploid resulting from the cross of tetraploids is very similar to *B. carinata* (54). Cabbage was used as the cole parent. Only two plants were fertile, and the seven F_2 plants were nearly self sterile. In spite of this the amphidiploid, which is named *B. pseudocarinata,* crosses readily as female with *B. carinata* (54).

B. CARINATA–B. NIGRA. If *B. carinata* originated as an amphidiploid of the cross *B. nigra–B. oleracea,* then *B. carinata* × *B. nigra* is in a sense a backcross. The pollination of 44 flowers resulted in 21 seeds and 17 hybrids (257). There are 25 somatic chromosomes. These give 8 pairs and 9 single chromosomes during meiosis. This is to be expected on the basis of the genomic formula (bbcc × bb = bbc). The plants are highly sterile. These results are confirmed by those of Mizushima (141) who also reports a chromosome doubling of this hybrid (142). This plant had 50 somatic chromosomes, and at meiosis there were 8 to 1 quadrivalent, 8 to 23 bivalent and 2 to 0 univalent chromosomes. This plant was 60 per cent fertile when self pollinated.

B. CARINATA–B. OLERACEA. *B. carinata* × *B. oleracea* is also a form of backcross. A total of 334 flowers resulted in 20 seeds and 14 plants (106). The reciprocal cross gave a single hybrid from 271 pollinations. Two hybrids from a direct cross had 26 somatic chromosomes and 9 pairs plus 8 single chromosomes at meiosis (141). Similar results were obtained by U (257). From 248

pollinations he obtained five hybrids and two maternals. Four hybrids had 26 chromosomes which gave 9 pairs plus 8 single chromosomes, and one plant had an extra genome of 9, totaling 35 chromosomes. *B. carinata* × tetraploid cabbage was easier to make (106), 408 pollinations yielding 776 seeds and 740 plants. In the reciprocal cross, 118 pollinations produced 55 seeds and 32 plants. The degree of success in this cross depends upon the individual plants of each species selected. After decapitation, chromosome doubling occurred in one per cent of the regenerated shoots (107). Only seven plants had a somatic chromosome number of 70, derived from $2 \times (17 + 18)$. One plant had 66 and the rest 62 to 65 chromosomes. Meiosis in the 70-chromosome plants was considerably more regular than in the 35-chromosome first generation. *B. carinata* ($n = 17$) × diploid cabbage ($n = 9$) had 9 pairs and 8 single chromosomes. *B. carinata* ($n = 17$) × tetraploid cabbage ($n = 18$) had up to eight trivalent chromosomes, each of which must have involved two cabbage and one *carinata* chromosome, as might be expected of a "backcross". Sexivalent groups forming chains and rings were found in the 70-chromosome plants. The pollen often had 35 chromosomes. The genomic formula is bbccccccc.

B. CARINATA–B. ALBOGLABRA. *B. carinata* × *B. alboglabra* is very similar to the preceding cross. Thirty-six pollinations yielded a single plant reported to have 25 somatic chromosomes (152), one less than expected. At meiosis 9 pairs and 7 single chromosomes were observed. The bivalents disjoin first; then the univalents divide. Second division is fairly normal. The M II plates have 13 to 17 bodies, with a mode of 15 and an average of 15.3. Six or seven chromosomes lag at A II.

8- AND 10-CHROMOSOME SPECIES AND THEIR AMPHIDIPLOIDS

B. NIGRA–B. CAMPESTRIS. An early attempt to cross *B. nigra* and *B. campestris* was unsuccessful (176). *B. campestris* × *B. nigra* yielded 22 hybrids with 18 somatic chromosomes (141). There are 0 to 3 pairs plus 18 to 12 single chromosomes. *B. nigra* × *B. campestris* var. *sarson* produced seven maternals (144). Five amphidiploid *campestris–nigra* plants had 36 somatic chromosomes and usually 18 pairs, rarely 17 pairs and 2 singles, at meiosis (142).

The plants were not self-fertile. Chopinet (31) reports that Ramanujam and Serinivasachai made the cross and doubled the chromosome number of the sterile F_1 to get a synthetic *B. juncea* in 1943.

B. NIGRA–B. RAPA. Like the *nigra–campestris* cross, the *nigra–rapa* combination proved unsuccessful (176). The cross *rapa* × *nigra* is similar to *campestris* × *nigra* and has probably been made (173), but, because the turnip is often referred to *B. campestris*, no definite reference can be given.

B. CERNUA–B. CHINENSIS AND B. RAPA. *B. cernua* Forb. & Hemsl. ($n = 18$) is introduced at this point because of its cytogenetic similarity to *B. juncea* and because Morinaga (149) first showed in a series of crosses with *B. cernua* that distinct species, such as *B. chinensis* and *B. rapa*, with the same number of chromosomes, behave very much alike in interspecific crosses, and, further, that the chromosome behavior of their respective haploid "set" or genome is very similar if not identical during meiosis of the first generation of comparable interspecific crosses. The first generation produces a few seeds on open pollination. There are 10 pairs and 8 single chromosomes at diakinensis and M I. The bivalents are spherical and are all on the metaphase plate. The univalents are bar-shaped and tend to be scattered. They do not divide unless on the plate. They often lag but find their way to the poles. Second metaphase has 10 to 18 chromosomes with a mode of 14 in the cross with *chinensis* and a mode of 15 in the cross with *rapa*. Chromosomes that split in the first division may split again in the second.

B. CERNUA–B. CAMPESTRIS. Forty-five plants ($2n = 28$) were obtained from *B. cernua* × *B. campestris* (aabb × aa = aab). As might be anticipated by this genomic formula, there were 10 pairs plus 8 single chromosomes at the first meiotic division (141). Four hybrids having double this chromosome number were obtained (142). Fertility is low—five to seven per cent, although the pollen appears to be normal.

B. CERNUA–B. NIGRA. Nineteen *B. cernua* × *B. nigra* F_1 plants with 26 somatic chromosomes have 8 bivalent and 10 univalent chromosomes at meiosis (141). The allopolyploid of this cross with two a and four b genomes has 52 somatic chromosomes. At

meiosis there are 7 to 2 quadrivalent, 10 to 22 bivalent, and 4 to 0 univalent chromosomes. The plants are self-sterile.

B. JUNCEA–B. NIGRA. *B. juncea* × *B. nigra* produced ten seeds, two of which germinated to give one maternal and one true hybrid (153). The ten bivalents suggested that *B. nigra* might be a parent of *B. juncea* in conjunction with *B. chinensis* or another 10-chromosome species. A later cross yielded nine hybrids ($2n = 26$), permitting confirmation of the meiotic situation (141). "Chinese mustard" is said to cross with black mustard (163).

B. JUNCEA–B. CAMPESTRIS. The cross *B. juncea* × *B. campestris* is only moderately difficult (173, 221). A total of 221 pollinations resulted in 120 pods and 372 seeds, 184 of which germinated. For individual crosses there were 0 to 81.5 per cent "good" seed. The first generation is more like *juncea* in habit. It is partially sterile. *B. juncea* × sarson appears to be less difficult (218). The F_1 plants ($2n = 28$) have 10 bivalent plus 8 univalent chromosomes. The latter sometimes split at A I. There are 13 to 18 chromosomes on the M II plates. A few seeds were obtained from open pollination. The reciprocal cross is more difficult. Sarson × Gay-toy gave a single seed from 11 pollinations (176). Sarson × Chinese greens and × Southern Curled mustard yielded no seed. Other workers (144), who obtained ten hybrids from the direct cross, got only one maternal from the reciprocal. Toria × ray (*campestris* × *juncea*) produced 14 maternal plants plus one with 20 maternal and 18 paternal chromosomes (194).

B. JUNCEA–ORIENTAL SPECIES. *B. chinensis* × *B. juncea* failed and the reciprocal cross was found either to fail or to be difficult to make, depending upon the material used (176). The cross between *juncea* and *parachinensis* is likewise difficult (221). The 159 pollinations gave 56 pods and 213 seeds, 7.6 per cent of which germinated. Only one true F_1 plant was obtained. This produced a second generation of 15 plants. The roots of all were thickened, white-fleshed and of turnip shape and flavor. They were fertile when self-pollinated and when crossed with *juncea*. No cytological examination of these plants is reported.

The pollination of 24 flowers of Chinese greens with pollen of Santosai (*B. pekinensis*) gave 12 pods and 12 seeds (176). The reciprocal cross was unsuccessful. Sinskaia (221) found *juncea–pekinensis* about as difficult as the cross with *chinensis*. There

were few seeds of poor quality. The F_1 is similar to *juncea* and highly sterile. The F_2 is also nearly sterile. Mizushima (141) obtained 35 hybrids from *juncea* × *pekinensis*, which had ten pairs and eight single chromosomes at meiosis. Nine allopolyploid *juncea–pekinensis* plants had five to seven per cent fertility (142). These 56-chromosome plants have the genomic formula aaaabb. At meiosis there are 6 to 1 quadrivalent, 13 to 26 bivalent, and 6 to 0 univalent chromosomes.

8- AND 12-CHROMOSOME SPECIES

B. NIGRA–B. HIRTA. There are two reports (165, 176) that black and white mustards do not cross. In one case (165) small pods but no seeds were obtained.

9-CHROMOSOME SPECIES

B. OLERACEA–B. KABER. Six plants were obtained from *B. oleracea* × *B. kaber* (*B. arvensis*) (141). There are 0 to 5 pairs and 18 to 8 single chromosomes at meiosis. There were three amphidiploid 36-chromosome plants of this cross (142), usually with 18 pairs and only rarely 17 pairs and 2 single chromosomes. The plants are self-sterile, although the pollen looks normal.

9- AND 10-CHROMOSOME SPECIES AND THEIR AMPHIDIPLOIDS

B. KABER–B. CAMPESTRIS AND B. RAPA. *B. campestris* × *B. kaber* combine the a and s genome. Twelve plants were obtained (141). It is perhaps surprising to find as many as five bivalents and 9 single chromosomes. The number of each varies between 0 and 5 and 19 and 9, respectively. The amphidiploid has 19 bivalent chromosomes at meiosis, but is reported to be sterile (142). The same results were obtained (141) for *rapa* × *kaber* as for *campestris* × *kaber*. The amphidiploid of this second cross is sterile. Chromosome behavior during meiosis is not reported.

B. KABER–B. PEKINENSIS. *B. pekinensis* × *B. kaber* is reported (142) only as an amphidiploid having 38 as the $2n$ number of chromosomes. It is not self-fertile.

B. OLERACEA–B. CAMPESTRIS. *B. campestris* × *B. oleracea* brings together the third combination of genomes, ac, possible among the three—a, b and c. Early attempts to cross the two species (106, 176) were negative, and Noguchi (169) found that in his material

the male nuclei entered the embryo sac, stimulating development without fertilization. A total of 732 pollinations resulted in 26 seeds, which germinated to give 11 maternals plus 4 true hybrids (257). The first generation is intermediate and up to the time of flowering is very similar to *B. napus*. Of the four F_1 plants, one was highly sterile, two were partially fertile, and one was completely fertile. They had 7.4, 39.8, 73.5 and 96.3 per cent good pollen. Somatic chromosome counts for each of the four plants were 19, 28, 29 and 38 chromosomes, respectively. Plant No. 1 averaged 9.2 bodies at M I, No. 2 averaged 16.6 (0 to 5 trivalent plus 4 to 9 bivalent and 5 to 10 univalent chromosomes), No. 3 averaged 14.5 bodies at M I, and No. 4 had 19 pairs of chromosomes. Meiosis for the fourth plant was regular. The chromosome situation in plant No. 3 was the same as in the cross *B. napus* × *B. campestris* (257).

Tetraploid *campestris* crossed with tetraploid cabbage gives *B. pseudonapus*, which greatly resembles *B. napus* (54). The two are very easily crossed. There are two sizes of pollen in both—in *napus* 30.9 and 35.0 microns, and in *pseudonapus* 33.7 and 37.9. Both have 19 pairs of chromosomes at the first meiotic division, with 18 pairs plus 2 single chromosomes in a few cells. The pollen of *napus* is 90 to 100 per cent normal, while *pseudonapus* has 35 to 80 per cent good pollen. The seeds of *pseudonapus* are smaller than those of *napus*.

B. NAPUS–B. OLERACEA. *B. napus* × *B. oleracea* and its reciprocal are difficult (25, 31, 165, 176, 209, 222, 257). A total of 207 kohlrabi flowers crossed with *napus* yielded seven seeds and only one plant (14). Of the reciprocal cross, 466 pollinations produced 23 seeds. Two-hundred-seventy pollinations of cabbage with *napus* gave 11 seeds. In subsequent seasons 423 flowers of *napus* × cabbage gave 165 seeds, and 270 flowers produced 243 seeds. The use of *napus* as seed parent was more productive than the reciprocal. Three-hundred-fifty-eight pollinations of *B. napus* var. *oleifera* L. × tetraploid cabbage resulted in 13 seeds and 7 hybrids, 1.9 hybrids per 100 flowers, while 124 reciprocal pollinations gave 5 seeds and 2 hybrids or 1.6 hybrids per 100 flowers (106). The cross has also been made by doubling the chromosomes of both species (30). The hybrids are more like *napus*, but the fertility is greatly reduced (257). There is about 30 per cent good pollen. The acc genomes are combined in this " backcross " type of cross.

The somatic chromosome number is 28 (10+9+9) (141). At meiosis there are 0 to 5 trivalent, 9 to 4 bivalent and 10 to 5 univalent chromosomes.

Work with *B. napus* var. *napella* × cabbage is more limited than with *napus*, but the results are similar. Two-hundred-eight pollinations gave no seed (106). The same number of *napella* flowers pollinated from tetraploid cabbage yielded 7 seeds and 3 hybrids—1.4 per 100 flowers.

B. NAPOBRASSICA–B. OLERACEA. Cabbage × rutabaga has been unsuccessful (176, 205, 231). There are some reports that the reciprocal cross is also unproductive (25, 165, 231), but rutabaga has been crossed successfully with kale and with cabbage (205). Backcrosses to the parental species were usually negative. A second generation was secured. No heads were obtained in either generation, but the leaves were like those of cabbage. Rutabaga-like roots were formed. No cytological results are reported.

B. NAPUS–B. CAMPESTRIS. In contrast to the *napus–oleracea* "backcross", *napus* × *campestris* and its reciprocal are easy to make (25, 142, 148, 257). One-hundred-forty flowers of *napus* × *campestris* yielded 2255 seeds and 303 hybrids (257). One-hundred-nineteen reciprocal pollinations gave 1569 seeds and 53 hybrids. The hybrid seed is smaller than that of the pure species (259). Some (31, 173) say the first generation is generally fertile, but others (142, 257) report only about ten per cent fertility. The hybrid has three genomes—aac. During meiosis there are 10 pairs and 9 single chromosomes (257). This represents complete pairing between chromosomes of the two a genomes, leaving the nine chromosomes of the c genome unpaired.

B. NAPOBRASSICA–B. CAMPESTRIS. We find only one report of rutabaga × "wild turnip" (25). Seventy-one seeds were obtained, an average of 2.6 per pod. Evidently the cross is not especially difficult.

B. NAPUS–B. RAPA. Both *B. napus* × *B. rapa* and its reciprocal cross appear to be less easy to make than *napus* × *campestris*, but still not very difficult (14, 25, 31, 38, 176, 240). The cross was first made in 1834 by Herbert (Kajanus, 92). It seems to be about as successful one way as the other. Apparently there is little or no advantage to the use of the species with the higher chromosome number as seed parent in this case. There is com-

plete pairing between chromosomes of the two a genomes, giving 10 bivalents, plus 9 univalent chromosomes of the c genome at meiosis. The univalent chromosomes lag, and some split at M I. The second division is normal, although occasional restitution nuclei are seen. *B. napus* × tetraploid *B. rapa* gave nine hybrids with 58 somatic chromosomes, and two plants with a somatic count of 39. The latter were somewhat sterile, but the former were relatively fertile, as might be expected of balanced allopolyploids. The reciprocal cross gave 106 plants with 39 somatic chromosomes.

B. NAPOBRASSICA–B. RAPA. There has been a good deal of interest in this cross because of the edible thickened root of both rutabaga and turnip, which is of considerable economic importance, and because of other parallel variations in the two species (28). According to Kajanus (92), swede was first crossed with turnip by Herbert in 1834. Rutabaga (swede) × turnip has some advantage over the reciprocal cross (91, 205). There was an average of 13.0 seeds per pod for rutabaga × turnip compared with 7.3 per pod for the reciprocal cross (25). The hybrids are vigorous and have very large roots (38). Many first and later generation hybrids of this cross develop hybrid tubercules which proliferate and produce a monstrous type (93). There is great variability in the second generation (55). Various proportions of normal and monstrous are obtained—10,077 normal to 1,772 monstrous, and 6,417 normal to 3,372 monstrous (93). Later generations become more uniform. The F_6 families have better balance, although some plants are still monstrous in form (38). One F_2 family, more uniform and vigorous than the others, had double the chromosome number of the F_1 plants (55). Ratios of 3:1, 15:1 and 63:1 for white versus yellow flesh appear in the second generation.

The first generation has a marked reduction of fertility (28, 55, 165, 231). During meiosis there are 0 to 3 trivalent, 12 to 7 bivalent and 0 to 7 univalent chromosomes; 1 trivalent, 9 bivalent and 7 univalent chromosomes were seen most often (28). This observation was based on the mistaken assumption that $2n = 36$ in *napobrassica*. The hybrid has aac genomes $(10 + 10 + 9)$. One would expect on this basis 10 bivalents and 9 univalents. The behavior of the univalents is complex and difficult to follow. Up to six secondary associations were observed (28). F_2 plants have 22 to 45 somatic chromosomes. Most common numbers are 27, 28, 29, 31 and 32. These plants are highly sterile (28). One F_1

plant gave a uniform F_2 family of 268 plants (55). Plants of this family are reported to have 56 chromosomes, although 58 are expected, $(19+10)\times 2$. This allopolyploid is called *B. napocampestris*. The genomic formula is aaaacc.

B. NAPUS–B. CHINENSIS AND B. PEKINENSIS. These crosses, considered empirically, also represent a form of backcross (aacc × aa = aac). The cross with *pekinensis* is easier than with *chinensis* (221) and can be made rather easily in either direction (176, 221). There are 10 bivalent and 9 univalent chromosomes at the first meiotic division (141, 210). Univalent chromosomes lag, and some split at A I. The second division is normal except for occasional restitution nuclei (210). Fertility of the second generation plants is highly variable. Of 39 F_2 plants, 9 were completely sterile, 12 were partially sterile, 12 were normally fertile, and 6 did not bloom the first year (221). Sixteen F_1 plants with a doubled chromosome number were obtained (142). The 58 chromosomes group themselves as follows: 0 to 1 quinquevalent, 9 to 0 quadrivalent, 0 trivalent, 8 to 21 bivalent, and 6 to 0 univalent chromosomes. There is about ten per cent fertility. The pollen appears to be good.

B. NAPOBRASSICA–B. NIPPOSINICA AND B. PEKINENSIS. These crosses have been successful only with *napobrassica* as seed parent (176, 210). In both cases there is complete pairing between the chromosomes of the a genomes, giving 10 bivalent and 9 univalent chromosomes (210). The second division is normal except for restitution nuclei. Meiosis in the second generation is somewhat surprisingly reported (210) to be similar to meiosis in the F_1 plants, but there are usually more bivalent chromosomes. This suggests that some of the chromosomal combinations may be unsuccessful.

B. RAPA–B. OLERACEA. This is, in general, the same type of cross as *campestris–oleracea*. The cross between *rapa* and *oleracea* is very difficult (14, 25, 31, 176, 231). In 1946, 132 pollinations of cabbage × *rapa* gave no seeds (14). The cross was again unsuccessful in 1947 and 1949. One hybrid plant was obtained from 281 pollinations of the cross kohlrabi × *rapa* but nothing from 206 reciprocal pollinations. Chopinet (31) says that *rapa* crosses rarely with *oleracea*. It is possible that *B. rapa* of both Becker (14) and Chopinet (31) is the species treated here as *B. campes-*

tris. *Brassica* " nabicol " is reported (61) to be the amphidiploid of a cross between kale and turnip. The *n* chromosome number is 18, and $2n = 36$.

The parallelism between rutabaga and turnip and their apparent relation to *B. napus* and *B. campestris*, respectively, has been pointed out. If this parallelism is valid, one might conclude that *B. napobrassica* originated from *B. napus*. There is also the possibility that the amphidiploid *B. napobrassica* might have resulted from a chromosomal doubling of the F_1 hybrid *B. rapa–B. oleracea*.

B. OLERACEA–ORIENTAL SPECIES. No record of a successful cross between *B. chinensis* and diploid cabbage has been found (31, 106, 176). *B. chinensis* × tetraploid cabbage is fairly successful (106, 109). The F_1 plants have 9 bivalent and 10 univalent chromosomes, and are sterile (109). One of the adventitious shoots following decapitation had a doubled chromosome number. This produced 30 plants after self-pollination. Of these 30 seedlings, one had 55 chromosomes, twelve had 56, two had 57, one had 58, and one had 61 to 63 chromosomes. The others were not examined cytologically. The 56-chromosome plants bloomed late and usually had 28 bivalent chromosomes at M I. The distribution was not always regular at A I.

Only maternals that were more vigorous than the seed parent were obtained from *B. oleracea* × *B. japonica* and the reciprocal cross (95). The maternals were not the result of accidental self pollination.

B. nipposinica × diploid cabbage proved unsuccessful, but seven hybrids were obtained from the pollination with tetraploid cabbage (106).

Cabbage × *B. pekinensis* is reported (176) to be unsuccessful. A few seeds were secured from the reciprocal cross (95). Pe-tsai × Cows-fodder produced a few plants favoring the seed parent in appearance (192). There was no second generation. Pe-tsai × cauliflower resulted in three plants, also similar to Pe-tsai (192). A second generation of 50 plants was very vigorous and sterile.

Fifteen plants were obtained of amphidiploid ($2n = 56$) *pekinensis-oleracea* (142). At meiosis there are 9 to 1 quadrivalent, 5 to 21 bivalent and 10 to 0 univalent chromosomes. Fertility is about two per cent. The pollen appears to be nearly perfect.

9- AND 12-CHROMOSOME SPECIES

B. KABER–B. HIRTA. White mustard × charlock failed completely (165, 176). Charlock × white mustard resulted in small pods but no seeds (165). Both direct and reciprocal crosses of the tetraploid forms of each species were entirely unsuccessful (256).

B. OLERACEA–B. HIRTA. Cabbage × white mustard could not be crossed (176). White mustard × kale resulted in 4 hybrids from 49 pollinations (260). They are very similar to the female parent but are hairless and waxy, and have stiff dark green leaves. They have 21 chromosomes in somatic tissue. The chromosomes remain unpaired at M I and are scattered on the spindle. The second division is fairly normal. The pollen is shrivelled.

10-CHROMOSOME SPECIES

B. CAMPESTRIS–B. TOURNEFORTII, GOUAN. Both direct and reciprocal sarson × *tournefortii* resulted in maternal type plants only (144, 175).

B. TRILOCULARIS–B. TOURNEFORTII. *B. tournefortii* × *B. trilocularis* resulted in 5 maternal plants and 2 hybrids from 25 pollinations (218). All plants were $2n = 20$. Pairing is quite variable at diakinesis, when there may be as many as three bivalent chromosomes, sometimes a trivalent and even a quadrivalent association. Twenty single chromosomes are most frequent. The author (218) suggests the possibility of structural hybridity.

10- AND 12-CHROMOSOME SPECIES

B. CHINENSIS–B. HIRTA. White mustard × Pak-choi and reciprocal produced no pods (176).

B. RAPA–B. HIRTA. White mustard × turnip resulted in small pods but no seed. The reciprocal cross set no pods (165).

Crosses Involving Amphidiploid Species with Others Having Unlike Genomes

8- AND 19-CHROMOSOME SPECIES

B. NIGRA–B. NAPUS AND B. NAPOBRASSICA. Pearson (176) was unable to cross *napus* with diploid *nigra*. *B. napus* × tetraploid *nigra* gave 19 plants, $2n = 35$, all more or less sterile, but with 25

per cent good pollen (256). The reciprocal was unsuccessful. The *napobrassica–nigra* combination was not successful (176).

9- AND 17-CHROMOSOME SPECIES

B. KABER–B. CARINATA. Abyssinian mustard × charlock yielded 38 plants, $2n = 26$ (141). This involves the b, c and s genomes. At diakinesis there are 0 to 8 bivalent and 26 to 10 univalent chromosomes.

9- AND 18-CHROMOSOME SPECIES

B. OLERACEA–B. JUNCEA. *B. juncea* and kohlrabi are reported to be intersterile (95). Pollen of *B. juncea* germinates with great difficulty on stigmas of *B. oleracea*, and pollen tubes that appear can scarcely penetrate the stigmatic surface (209). *B. oleracea* Toyoda-Wase × *B. juncea* produced no seeds (209).

B. juncea × diploid cabbage is very difficult (95, 194). *B. juncea* × tetraploid cabbage resulted in seven hybrids, an average of 2.2 plants per 100 pollinations (106).

B. KABER–B. JUNCEA. *B. juncea* × *B. kaber* is very difficult (141, 176). Only one hybrid is reported (141). At meiosis there are 7 to 10 bivalent and 13 to 7 univalent chromosomes. This is a combination of a, b and s genomes.

9- AND 19-CHROMOSOME SPECIES

B. KABER–B. NAPUS AND B. NAPOBRASSICA. The crosses between the amphidiploid *napus* and *napobrassica* and diploid *kaber* are difficult (141, 176). A single plant ($2n = 28$) was obtained from *napus* × *kaber*, combining the a, c and s genomes. Chromosome behavior leads to 0 to 2 trivalents, 10 to 6 bivalents and 6 to 28 univalents at diakinesis (141). *B. napus* × tetraploid *kaber* failed completely (256).

10- AND 17-CHROMOSOME SPECIES

B. CAMPESTRIS–B. CARINATA. The 11 F_1 plants ($2n = 27$) of *B. carinata* × *B. campestris* combine the a, b and c genomes (141). During meiosis there are 0 to 9 bivalent and 27 to 9 univalent chromosomes. The allopolyploid of this cross has 54 chromosomes in somatic tissue. The genomic formula is aabbcc. At diakinesis there are 7 to 0 quadrivalents, 11 to 27 bivalents, and 4 to 0 that

are single (142). The fertility is about 50 per cent. All of the pollen appears to be normal.

B. RAPA–B. CARINATA. Two hybrids were obtained from *B. carinata* × *B. rapa* (151). They produced a few seeds on open pollination. There are 1 to 9 pairs and 25 to 9 single chromosomes at the first meiotic division. The second division is fairly regular. The second metaphase plates have 11 to 18 chromosomes.

B. CHINENSIS–B. CARINATA. *B. chinensis* × *B. carinata* gave six plants with $2n = 27$ (151). They were more like *carinata*. A few seeds were obtained from open pollination. Chromosome behavior is the same as described for *carinata–rapa*. The F_1 plants of *B. chinensis* × *B. carinata* obtained by Howard (83) produced a large number of good seeds. The plants were treated with colchicine to double the chromosome number. The few resulting allopolyploids were almost completely sterile. A second generation had a $2n$ chromosome count of 55 instead of the 54 expected. There were about 27 bivalents at the first division of meiosis, and 26 to 29 chromosomes on the M II plates. Bridges were observed at A I in both the original F_1 plants and in those with 55 chromosomes. Some of the bridges persisted to A II. Fertility of the 55-chromosome plants was 50 to 100 per cent. Howard (83) thinks that genes for incompatibility obtained from *chinensis* are active in the allopolyploids. The allopolyploid crosses readily as female with *carinata* and diploid *chinensis* but is unsuccessful as pollinator on these species. Tetraploid *chinensis* is fertile in reciprocal crosses with the allopolyploid. Only a few good seeds were obtained from *carinata* × *chinensis*. Use of the species with the higher chromosome number as female parent did not reduce the difficulty of making the cross.

B. PEKINENSIS–B. CARINATA. *B. pekinensis* × *B. carinata* gave eight maternal plants (86). The reciprocal cross produced 2 hybrids in addition to 12 maternals. Lobing of the leaves of *carinata* is dominant to the entire sessile leaves of pekinensis. The allopolyploid was produced both by colchicine treatment of the F_1 plants and by crossing forms of each species with double the chromosome number. The F_1 plants of the original cross, with three genomes (a b c) and $2n = 27$, had 0.4 per cent viable pollen. The allopolyploid has 32.5 to 42.9 per cent viable pollen. It had three to eight

viable seeds per pod, compared to 13 for the parental species. Mizushima (142) obtained one allopolyploid from this cross.

12- AND 18-CHROMOSOME SPECIES

B. HIRTA–B. JUNCEA. *B. hirta* (white mustard) × *B. juncea* Gai-toy and white mustard × *B. juncea* Chinese greens were both unsuccessful (176).

12- AND 19-CHROMOSOME SPECIES

B. HIRTA–B. NAPUS AND B. NAPOBRASSICA. Direct and reciprocal crosses between *B. hirta* and both *B. napus* and *B. napobrassica* were unsuccessful (165, 176). The latter produced small pods but no seeds (165). *B. napus* × tetraploid *hirta* failed completely (256).

17- AND 18-CHROMOSOME SPECIES

B. CARINATA–B. JUNCEA. The cross *B. juncea* × *B. carinata* is between two essentially amphidiploid species. One-hundred-forty-one pollinations gave 448 seeds and 24 hybrids plus 2 maternal plants (257). Ninety-four pollinations of the reciprocal cross produced six seeds but no plants. The F_1 plants are more like *carinata*. They are partially fertile, yielding on open pollination over 100 seeds each, although they did not set pods under paper bags. The somatic chromosome number is 35. There are 8 to 16 bivalents and 18 to 3 univalents at M I. Genomic formula of the hybrid is abbc.

17- AND 19-CHROMOSOME SPECIES

B. CARINATA–B. NAPUS. Fifty-five flowers of *B. napus* × *B. carinata* gave one maternal and one true hybrid (257). The reciprocal cross yielded three seeds but no plants. The single hybrid was more like *napus*. It was partially fertile. There are at diakinesis 0 to 6 trivalent, 9 to 3 bivalent and 18 to 12 univalent chromosomes. The four genomes involved are abcc.

18- AND 19-CHROMOSOME SPECIES

B. JUNCEA–B. NAPUS AND B. NAPELLA. Crosses of *juncea* with both *napus* and *napella* are relatively easy and give partially fertile F_1 plants (31, 176, 210, 221). *B. juncea* × *B. napus* is easier than the reciprocal (176). Olsson (173) reports that the F_1 plants are

sterile. Sinskaia (221) obtained some completely sterile F_1 plants and secured no seeds under bags from any F_1 plants. Many plants, especially new types, in the second generation were found to be sterile. The cross of *juncea* Tai-chich-tsai and *napobrassica* Ching-tsai has 10 pairs plus 17 single chromosomes. This represents pairing between the two 10-chromosome a genomes, since the cross is aabb × aacc = aabc (10 + 10 + 8 + 9).

B. CERNUA–B. NAPELLA. *B. cernua* × *B. napella* is empirically the same type of cross as *B. juncea* × *B. napella* or *B. napus*. There are 10 pairs and 17 single chromosomes as before (150).

ERUCA SATIVA MILL. ROCKET-SALAD, ROCKET OR ROQUETTE

Rocket originated in southern Europe (10), where it was abundant in gardens in the 16th century (228). Although introduced into the United States before 1854 (228), it has never become popular.

There are 22 somatic chromosomes (135). Pairing is complete during diakinesis and M I, with 11 bivalent chromosomes (2). Its haploid set of chromosomes has been designated the " e " genome (260). Nine hybrids were secured from *B. chinensis* × *E. sativa*. The *2n* chromosome number is 21 (10 + 11). At the first meiotic division there are 0 to 8 bivalent and 21 to 5 univalent chromosomes (141). Four plants with 42 somatic chromosomes were obtained (142). There are 21 pairs of chromosomes at the reduction division of these plants. Six hybrids intermediate in appearance were obtained from *E. sativa* × *B. oleracea* (260). There are 0 to 3 bivalent and 20 to 14 univalent chromosomes at diakinesis. Three pairs were seen most frequently. Behavior of the single chromosomes is " remarkably abnormal ", a good many remaining on the metaphase plate. The authors (260) suggest that the three bivalents may represent pairing among *oleracea* chromosomes. The following chromosomal formula has been suggested for the e genome: AABBCCDDEEF (2). The F chromosome is considered to be the result of chromosomal fusion.

RAPHANUS SATIVUS L. RADISH

Origin and History

It is generally agreed (27, 228, 252, 264) that China is the most important region of origin of the radish. It was illustrated by a

disciple of Confucius in 450 B.C. (252), and was known to the early Egyptians and Greeks (228, 252). Another region of importance is the central Asiatic center including northwest India and adjacent areas to the north and west (264). The radish is now very widely grown. It has been feral in southern Europe for a considerable period (228). There are many varieties. Those eaten fresh in America and Europe are comparatively small, but the prevailing oriental kinds, which are brined, are large to very large (20, 228). *Raphanus sativus* var. *caudatus* Linn., the long fleshy pods of which are eaten, is native to eastern India and Burma (264). One type is grown for its oil-bearing seeds (228), another is used for greens (20). Investigation of an early claim that the radish, *R. sativus*, can be developed from the thin-rooted *R. raphanistrum* L. by selection indicates that the original selections followed natural crossing between the two species (252). This natural cross also occurs in California (56). The cross can be readily made (253).

Genetics

EXTERIOR ROOT COLOR. Yellow is a simple dominant to white (130, 261) in some crosses and gives a dihybrid ratio in Round Yellow × Early White. Anthocyanin color in the exterior of the root results from the presence of cyanoplasts contained in the outer layers of cells (186). Their number and size vary from one cell to another. Results of crosses among different types of anthocyanin colors also appears to depend upon the varieties crossed. Simplest is dominant purple $R \times$ red r (*sativus-raphanistrum*), which segregates 3 purple to 1 red (56). Crosses between red and white segregate 1 red : 2 purple : 1 white (261). A later report (172), only the abstract of which has been seen, utilizes three genes. Red is R_2R_3cc, purple is $R_2r_3r_3C$ or $r_2r_2R_3C$ and white is $r_2r_2r_3r_3Cc$. R_2 and R_3 are lethal when either is homozygous.

Tatebe (235, 237, 239), in a series of papers seen only in abstract, proposes other designations for genes controlling exterior root color: red, Rby; purple, RBy; yellow, rBY; black, rBY^b; white, rBY; and blackish purple, RBY^b. Y^b is dominant to Y, which in turn is dominant to y. Red $RRbbyy \times$ black $rrBBY^bY^b$ gives blackish purple in the first generation and an F_2 segregation of 27 blackish purple : 9 purple : 9 blackish-red : 3 red : 12 black : 4 white. These designations were later (237) modified to the fol-

lowing: red, *Ry*; purple, R^py; yellow, *rY*; and white, *rryy*. Red and purple are epistatic to yellow. The gene *G* gives pale green neck or hypocotyl; *vg*, white neck; and R^s, red striping. *R*, R^p, R^s and *r* all form an allelic series (239).

Red striping on a white background, $R \times$ white *rr*, gives a 1:1 ratio (261). This is a consequence of lethal homozygous *R R*. If the priority of Frost's gene *R* for purple vs. *r* for red is to be recognized, Uphof's gene for red striping might appropriately be redesignated *Rs*, or R^s if it is the equivalent of the gene studied by Tatebe. The inheritance of black in a cross with red could not be determined from an F_2 population of 180 plants (261). Red $\times$ black gives a deep violet (254).

OTHER COLOR FACTORS. A seedling character, reddish cortex, appears in crosses with the variety Long White. The color disappears as the plants mature. The character is determined by duplicate dominant genes, resulting in an F_2 ratio of 15 with red cortex to 1 white (261). These factors are designated R_1 and R_2. When either is homozygous dominant and the other homozygous recessive, a cross with white segregates 3:1. The yellow flowers of *R. raphanistrum* were recessive to white or white tinged with rose in most F_1 plants (254, 255). In a few of the plants the environment favored a partial development of yellow. The yellow corolla of *Brassica oleracea* is recessive to white in crosses with radish (57). White is dominant to white tinged with rose or lavender (254).

Shape of Root. Extremes of root shape are short spherical or round and long cylindrical. Crosses between two homozygous types show a single gene difference, with an intermediate F_1 and a 1:2:1 F_2 ratio (238, 261). Other work (130) indicates that a series of partially dominant genes, L_1, L_2, etc., distinguishes between long and short roots. Important intermediate shapes are conical and oval. The thin root of *raphanistrum* is nearly dominant to the fleshy root of *sativus* (252). A few F_2 plants have a thicker root than the F_1 plants. One-fourth of the plants of the Scarlet Globe, White Box and White Icicle varieties had a thin tap root when grown at high temperature and humidity (13).

OTHER CHARACTERS. Selection among plants grown during hot weather for firmness of root vs. spongy tissue and for delayed flowering were successful, demonstrating a genetic basis for both

characters (116). Length of day is important in determining flowering. The radish is a long-day plant. The corky epidermal layer of the black (winter) varieties is dominant to the smooth epidermis found in the spring and summer varieties (261). The cross between *raphanistrum* with comparatively little sugar in the root and *sativus*, which is high in sugar, gives F_1 plants with at least as much sugar in their roots as in radish (254). The woody silique of *raphanistrum* is dominant to the papery pod of *sativus* with a complex segregation (56). Foliage may be relatively scant, abundant or intermediate. Long Red (abundant foliage) × Early White (scant foliage) gave F_1 plants with intermediate foliage and a second generation that segregated 1:2:1 (261). The early flowering *raphanistrum* crossed with the later flowering radish produced a first generation that approached the early flowering of *raphanistrum* (56).

INCOMPATIBILITY. Individual plants of both *R. raphanistrum* (56) and *R. sativus* (130) vary in their degree of self-compatibility. When the flowers are protected there are 0 to 270 seeds. Pollen may germinate slightly on stigmas of self-incompatible plants of the Japanese radish, but it makes little growth (240). Bud pollination of self-incompatible plants gives normal germination and growth of about 90 per cent of the pollen, although pollen tube growth is somewhat slower than in compatible combinations. Removal of a thin layer of the stigma removes most of the inhibiting substance. The effectiveness of the inhibiting substance decreases with increasing age of the flower (240).

DISEASE RESISTANCE. All commercial varieties of radish are susceptible to Fusarium wilt, caused by race 2 of *Fusarium oxysporum* f. *conglutinans* (Wr.) Snyd. & Hans. (189). Resistant lines have been selected from the Scarlet Globe variety. Most commercial varieties of radish are resistant to a mosaic disease of rape, but Chinese radish is susceptible (123).

MALE STERILITY. Three male-sterile plants were found in the Tokinashi variety of Japanese radish (248). Meiosis is normal to diakinesis, when the pollen mother cells degenerate rapidly. The pistils are normal in appearance and function normally, although seed production is somewhat reduced. The petals are usually reduced in size. The character is inherited as a simple recessive, *ms.*

Segregation in the second generation was 251:70, and the backcross produced 239:237.

Cytology

The somatic chromosome number of *R. sativus* and its varieties is 18 (253). *Raphanus raphanistroides* Nakai has the same number (223). The nine somatic chromosomes of the radish genome are placed in six morphological groups (201) as follows:

Type	Length (microns)	Constriction	No. of chromosomes
A	2.4–2.5	Submedian	1
B	2.0–2.3	Median	1
C	1.5–1.7	Subterminal	1
D	1.4–1.7	Submedian	2
E	0.9–1.1	Subterminal	1
F	0.9–1.1	Submedian	2

The Indian radish, a form of *R. sativus,* has nine bivalent chromosomes at diakinesis (230). Meiosis is normal (201, 230). Occasional single tetravalent and even sexivalent chromosomes have been observed at diakinesis of Japanese varieties (126). All chiasmata terminalize by M I. Two or three bivalents sometimes exhibit secondary association at diakinesis (236). This may result in four groups of chromosomes (201). A good many associations involve two pairs of chromosomes, and there are several of three pairs, probably B, D and F. Association of different types is explained by structural hybridity. Doubling the chromosome number of radish increases the size of the plant but not seed production (219). There are occasional tetravalents in recent tetraploids, but these are not seen in crosses between tetraploid varieties (242). Tetraploid plants have a more vigorous root system and are more resistant to cold than comparable diploids (168).

INTERGENERIC HYBRIDS INVOLVING *RAPHANUS* AND *BRASSICA*

R. sativus–B. oleracea

The classic intergeneric cross between radish and cabbage was first made by Sageret in 1826 (cited by Kakizaki, 96). It was next made by Gravatt (66) in 1914, who pollinated flowers of Long Scarlet Short Top with pollen of a cross between Volga and Savoy cabbage. The reciprocal cross produced only shrivelled

seeds. The single F_1 plant exhibited great hybrid vigor but was completely sterile. This and similar crosses were made by several workers during the 1920's—Baur (cited by Kakizaki, 96), Karpechenko (101), Moldenhawer (146), Kakizaki (96) and Fukushima (57), who also secured a single plant from Succession cabbage × Japanese radish. U, Midusima and Saito (258) were later successful in crossing kitchen kale × Japanese radish.

FIRST GENERATION. Karpechenko (101) crossed radish with three coles—cabbage (including savoy), kohlrabi and brussels sprouts. Three plant types appeared in the F_1: (*a*) small plants with short, often branched stems with short flowering shoots, and many small leaves, (*b*) big leafy rosettes 1.5 meters in diameter, or short bushes with big leaves, and (*c*) tall vigorous plants with long flowering shoots. Both the second and the third type were larger than either parent. All three plant types appeared in all three crosses. About half of the plants from the kohlrabi cross had enlarged stems but the cross with cabbage produced no heads. The roots were branched instead of being fleshy, but had " peculiar outgrowths of different shapes and size . . . ". Most of the hybrids had leaves of intermediate type. The small plants usually had leaves more like the radish type, and the largest plants had leaves more like the cabbage type. These plants flowered much more abundantly than did either parent. White-flowered radish crossed with yellow-flowered cabbage produced F_1 plants with white, purple or cream flowers. The lower portion of the silique is similar to that of cabbage, while the upper portion is similar to that of radish. Its appearance depends to a considerable extent upon seed development, which was very limited in most of Karpechenko's plants. They were considered to be sterile.

There is no pairing during meiosis in the F_1 pollen mother cells. This results in 18 single chromosomes at diakinesis and M I (101). The first metaphase plate is abnormal. The univalent chromosomes usually move to the poles without dividing. Distribution apparently is at random. Second division begins during telophase but is much more normal than the first division. A poorly defined spindle is usually present at A II. There may be up to seven microspores. A few normal-appearing pollen grains are found. The number of chromosomes reaching the poles at second division is usually 6 to 12. Occasionally all 18 chromosomes remain near

the middle between the poles at first division, A I failing. They may then split to produce two 18-chromosome diads. If the division is normal, two functional pollen grains then develop. There may also be a few gametes with 36 chromosomes. The most common number approaches the haploid, with a few diploid and an occasional tetraploid microspore (101).

While Karpechenko (101, 104) did not observe pairing in PMC of F_1 plants, U, Midusima and Saito (258) found 2 or 3 loosely paired bivalents, and Richharia (201) observed up to 9 bivalents at M I, with a mode of 4. He thinks there may be pairing both between and within genomes. Fukushima (57) found as many as 6 pairs, although 2 or 3 pairs occur most often, and the 18-chromosome F_2 plants examined by Piech and Moldenhawer (185) had 4 to 8 bivalents at diakinesis. They followed their material through the fourth generation. In every case only four microspores, each of which had 6 to 10 chromosomes, developed. No double diploids were obtained. Howard (79) also reports up to 6 bivalents in additional material of the cross described by Richharia (201). Two pairs were most frequent. Howard (79) also observed a secondary type of association between univalents. He found pairing between morphologically diverse chromosomes and, in addition, chromosome bridges in many cells. He regards the bridges as the result of inversions.

Meiosis is also abnormal in the egg mother cells (101). There is some pairing. One cell was observed to have nine pairs of chromosomes.

SECOND GENERATION. Moldenhawer's four second generation plants exhibited considerable variation (146). They had the diploid chromosome number (185). The crosses reported by Richharia (201) and by Howard (79) also had a considerable number of plants with somatic chromosome numbers less than 36. The lowest chromosome number of Karpechenko's second generation was 27, the triploid number (103). A total of 361 F_2 plants was grown, 229 of which were examined cytologically, with the following $2n$ numbers of chromosomes and the number of plants of each: 27—1, 36—213, 36 or 37—4, 36 to 38—4, 38—3, 41—1, 51—1, 51 to 53—2. Thirteen F_1 plants bloomed in the field close to radish. Chromosome counts of 73 plants resulting from open pollination were made. Sixty-one had the $3x$ number and the

others had higher numbers up to 53. These results led Karpechenko to conclude that pollen with less than 18 chromosomes failed to function in the F_1 plants. Seeds produced the second season gave 452 F_2 plants (102). Many of these had a somatic chromosome number of 36.

The relation of the $3x$ plants with two radish plus one cabbage genome to other forms can most conveniently be gauged by noting the number of seeds per 100 pollinations in crosses: $3x \times 3x$, 16.1; $3x \times$ radish, 386.6; $3x \times$ cabbage, 16.3; $3x \times 4x$, 0; $3x \times 5x$, 3.5; $3x \times R.$ *raphanistrum*, 0; $3x \times B.$ *napus*, 0; $3x \times B.$ *campestris*, 0 (103). In contrast to this, $5x$ plants produced no seeds with radish, cabbage, $3x$, $5x$, *B. alboglabra*, *B. napus* or *B. chinensis*. The cross $5x \times 4x$ gave 4.2 seeds per 100 pollinations. The $3x$ plants had 9 bivalents and 9 univalent chromosomes (103, 258). This represents pairing between the two radish genomes.

The proportion of the silique that is bivalve depends upon the number of cabbage and radish genomes that occurs in a hybrid (102). Where these are balanced, as in the $2x$, $4x$ and $6x$ plants, about half of the silique is bivalve. In $3x$ with two radish genomes this proportion decreases to one-third.

THE AMPHIDIPLOID. The $4x$ plants are larger than $2x$ F_1 plants (103). In contrast to the first generation, most $4x$ second generation plants are fertile. A few such plants exhibited reduced fertility in spite of regular meiosis and normal pollen. These plants also proved to be sterile in crosses. In general, cabbage dominates in structure of the principal organs, as the stem, root and seed (67). The leaves are intermediate, although the epidermal cells may be like those of radish. Howard's (79) $4x$ second generation plants were less fertile than Karpechenko's. Seven secondarily associated groups were observed most often. Meiosis of the amphidiploid is quite normal, usually with 18 bivalents at M I (102). There is an occasional univalent, trivalent or quadrivalent chromosome (79). Secondary association is " very marked ". The M II plate usually has 18 chromosomes, but there may be 16 to 19. Somatic chromosome numbers in the next generation were 33 to 37. These plants had 86 to 96 per cent good pollen.

The amphidiploid from a cross between tetraploid radish and cabbage is intermediate in appearance and behaves about like the

original (113, 215). Most plants have 18 bivalents at meiosis, although one plant had 17 pairs and one single chromosome, and another had 18 pairs plus one chromosome (113). In spite of its great height (eight feet when in fruit), the plant is unsatisfactory for either oil or forage (33). No self-incompatible plants have been found in *Raphanobrassica* (84).

CROSSING RELATIONS OF THE AMPHIDIPLOID. The following data are in terms of the number of seeds per 100 pollinations: $4x \times$ radish, 1.6; $4x \times$ cabbage, 0.9; $4x \times 3x$, 0; $4x \times 4x$, 42.4; $4x \times 5x$, 7.4; $4x \times$ *R. raphanistrum*, 13.3; $4x \times$ *B. alboglabra*, 0; $4x \times$ *B. campestris*, 0; $4x \times$ *B. chinensis*, 0; $4x \times$ *B. napus*, 0. Reciprocal crosses with tetraploid cabbage produced a few plants with white flowers and no head that bloomed the second season (106, 108). The plants had 36 somatic chromosomes and were sterile. They have one radish and three cabbage genomes. As a result, two-thirds of the length of the silique is bivalve. Meiosis is irregular with univalent, bivalent and trivalent chromosomes. The nine radish chromosomes always remain single. The amphidiploid *Raphanobrassica* has also been crossed with octoploid cabbage as seed parent (215). Most plants had 54 somatic chromosomes—one radish plus five cabbage genomes. One plant had 45 chromosomes, combining one radish with four cabbage genomes.

Raphanobrassica ($n = 18$) has been found to cross with seven species of *Brassica* (106). Results depend upon the individual plants involved. It crosses quite readily with *carinata* ($n = 17$), with *napus* ($n = 19$) and *napella*. It also crosses with *campestris*, *chinensis* and *nipposinica* (all $n = 10$), and with *juncea* ($n = 16$). Number of plants obtained in various crosses follows: *Raphanobrassica* $\times$ *B. carinata*, 57; reciprocal cross, 38; $\times$ *napus* subsp. *rapifera*, 2; reciprocal cross, 10; $\times$ *napus* subsp. *oleifera*, 1; reciprocal, 0; $\times$ *pekinensis*, 2; reciprocal, 0; $\times$ *campestris* subsp. *rapifera*, 1; reciprocal, 0; and crossed reciprocally with *campestris* subsp. *oleifera*, *alboglabra*, *chinensis*, *hirta*, *kaber* and *juncea*, 0 (105). Crosses of *Raphanobrassica* with *Eruca sativa*, *Erucastrum incanum* and with *Raphanistrum rugosum* were unsuccessful. *Raphanobrassica–B. carinata* has 9 to 17 bivalent and 17 to 1 univalent chromosomes at meiosis, and *Raphanobrassica–B. campestris* has 5 to 6 bivalent and 18 to 16 univalent chromosomes (105).

R. sativus–B. alboglabra

B. alboglabra × *R. sativus* is easier to make than is *B. oleracea* × *R. sativus* (59). Some weak F_1 plants died early; those remaining were vigorous.

R. sativus–B. kaber

Both diploid and tetraploid radish and charlock have been crossed successfully (141, 142). The diploid F_1 plants have 0 to 3 bivalents and 18 to 12 univalents (141). The amphidiploid ($2n = 36$) has 18 bivalent chromosomes.

R. sativus–B. campestris

Raphanus sativus × *B. campestris* gave plants with 18 somatic chromosomes which had one to three loosely paired bivalent chromosomes at meiosis (258). One plant had 28 chromosomes with 9 bivalent and 10 univalent chromosomes at M I.

R. sativus–B. rapa

A total of 162 F_1 plants was obtained from turnip × radish, and 23 plants from the reciprocal cross (141). Up to 5 pairs with 19 to 9 single chromosomes have been observed in the direct cross. Its reciprocal had 0 to 3 bivalent plus 19 to 13 univalent chromosomes. The amphidiploid ($2n = 38$), of which there were 104 plants, has 19 bivalent chromosomes. One plant from tetraploid *R. sativus* × *B. rapa* had 56 chromosomes, combining four radish genomes with two of turnip. At meiosis there is an occasional hexivalent, 9 to 0 quadrivalent, 8 to 28 bivalent and 4 to 0 univalent chromosomes (142). Radish × turnip produced one plant with 28 (?) somatic chromosomes (162). There appeared to be 9 pairs plus 10 single chromosomes, which lagged. This plant flowered adjacent to *B. oleracea, rapa, chinensis, pekinensis, napobrassica* and radish. Progeny from open pollination was a variable lot with $2n$ chromosome numbers of 18 to 56. The backcross with radish gave 18-chromosome radishes plus one 19-chromosome plant.

R. sativus–B. chinensis

B. chinensis × *R. sativus* has twice been reported to be successful (157, 244). The sterile first generation is intermediate and has 19 somatic chromosomes. Terasawa (244) obtained 7 amphi-

diploids among 58 F_4 plants. The amphidiploid is also intermediate in appearance. The leaves are lobed, roots are fleshy, and flowers are white with purple veins. Most of the plants are fully fertile. Four of 41 F_5 plants exhibited some irregularities during meiosis. Six F_5 plants were unusually fruitful and gave 9 to 112 F_6 plants each.

R. sativus–B. pekinensis

The cross was successful when *B. pekinensis* was used as female parent (245). Chromosome doubling produced the amphidiploid *Brassicoraphanus*. It is fully fertile when self-pollinated. When used as seed parent, a few plants were produced with *R. sativus, pekinensis, chinensis, oleracea, cernus* and *napus*.

R. sativus–B. carinata

Karpechenko (105) reports one plant from 58 pollinations of *B. carinata* × *R. sativus*. Fukushima (58, 59) secured three highly sterile hybrids from this cross. This combines three genomes, b and c from Abyssinian mustard and r from radish. The F_1 plants have 26 somatic chromosomes. At meiosis there were 0 to 4 bivalent chromosomes (0 in 8 cells, 1 pair was found 15 times, 2 pairs 43 times, 3 pairs 34 times and 4 pairs were observed in 16 cells).

Richharia (203) secured vigorous hybrids. Fruits have the basal two-thirds dehiscent (bivalve) and the remainder indehiscent. There are 6 to 9 bivalents at diakinesis, and 2 to 9 at M I. Secondary association between bivalents and univalents is frequent, especially when there are nine pairs. The plants are very sterile with only one to two per cent of good pollen. A single 28-chromosome F_2 plant was obtained. There are usually 5 to 10 bivalents and the rest univalents. Homotypic metaphase plates may have $10+18$, $12+16$, or $14+18$ chromosomes. There is 7 to 14 per cent of large pollen and 86 to 93 per cent small pollen.

R. sativus–B. cernua

B. cernua var. Karashi × *R. sativus* var. Minowase is vigorous, more or less intermediate and completely sterile (57, 59). The somatic chromosome number is 27. The cross combines the a, b and r genomes. There is no pairing at M I. The second meta-

phase plates have 14 to 20 chromosomes; division is normal. Four to ten chromosomes split twice. Pollen forms but degenerates.

R. sativus–B. juncea

B. juncea × *R. sativus* gave two sterile plants with 27 somatic chromosomes (57, 59). There is no pairing at diakinesis; some chromosomes split at M I. Second metaphase plates have 14 to 20 chromosomes. Apparently no chromosome divides twice.

R. sativus–B. napus

Numerous pollinations of *R. sativus* with pollen of *B. napus* and its variety *napella* as well as the reciprocal cross were completely unsuccessful (59). However, Chopinet (30) secured seven hybrids from this cross. The plants are very vigorous and intermediate in appearance. The amphidiploid has a regular meiosis and is stable.

CRAMBE MARITIMA L. SEA-KALE

Crambe maritima L. is a Mediterranean species (264). It is a salad plant little grown in the United States. The somatic chromosome number is 60 (135). Related species have 30 to 120 chromosomes. Sea-kale has been successfully grafted on "chou forrager", probably *B. oleracea acephala* (34).

LEPIDIUM SATIVUM L. GARDEN CRESS

The primary center of origin of *Lepidium sativum* L. is in Abyssinia, with secondary centers in Asia Minor and Iran to northwestern India (264). It is of ancient use as a salad plant in Iran, Greece and Egypt. Its somatic chromosome number has been reported to be 16 (87, 135) and also 24 (262). Related species have 16, 24, 40 and 64 chromosomes (135). Vaarama (262) thinks that the primary basic number for the genus is four and that the species are characterized by "cryptic polyploidy". Meiosis is very regular. The pollen is good.

ARMORACIA LAPATHIFOLIA GAERTN., MEY., & SCHERB. HORSE-RADISH

This native of eastern Europe was first grown for medicinal use, but both leaves and roots were eaten in Germany during the Middle Ages (228). Its somatic chromosome number is 32 (135). Common horse-radish is male-sterile, but the smooth-leaved Bo-

hemian horse-radish from southeastern Europe produces some pollen (77). The latter is resistant to white rust, caused by *Albugo candida* (Pers. ex Chev.) Kuntze (77). There is a wide range of resistance in the first generation of a cross between common and Bohemian forms. Some plants had greater resistance than Bohemian. Other plants were more susceptible than common horse-radish. Of 169 F_4 plants, 4 had about the same resistance as Bohemian, 3 had more, and 162 had less resistance than the common type. Bohemian self-pollinated gave 9 plants with resistance like itself, 8 with greater resistance, and 31 with considerably less resistance. Tests for resistance were made in the greenhouse.

NASTURTIUM OFFICINALE R. BR. WATER-CRESS

Nasturtium officinale R. Br. was grown as a medicinal plant from the first to the nineteenth century (136), and as a salad plant in Europe "from time immemorial" (228). Its diploid chromosome number is 32, but there are triploid and tetraploid forms. Brown water-cress, the triploid, is a cross between tetraploid and diploid (85). The chromosomes of green water-cress, the diploid, have been doubled to give a tetraploid form (85). Fruits of the tetraploid are larger than those of the diploid. It is fully fertile. Meiosis is regular with 32 bivalents at diakinesis (136). The triploid is nearly sterile.

SOME GENERAL CONSIDERATIONS

Chromosome association in *Brassica* and related genera is of three fairly distinct types. First we have the intimate pairing between homologs that is normal for balanced diploids. Secondly there is pairing between related chromosomes in species hybrids, that has a similar basis and shows an evolutionary relationship between the two species. Finally a loose secondary association is seen between two or more bivalent chromosomes. The evolutionary significance of the secondary association is less clear and less well established than the other two types.

Association of the second type has led to the grouping of genomes of the more closely related species. Six such groups of genomes have thus far been established. These are listed with representative species and chromosome number: the a genome—

Brassica campestris ($n = 10$), b—*B. nigra* ($n = 8$), c—*B. oleracea* ($n = 9$), e—*Eruca sativa* ($n = 11$), r—*Raphanus sativus* ($n = 9$), and s—*B. kaber* ($n = 9$) (originally *Sinapis arvensis*). It seems logical to consider *B. hirta* with 12 chromosomes as establishing a seventh " d " group.

The discovery of amphidiploid species whose double genomes could be identified with genomes found in diploid species gave much support to this grouping of genomes. The listing can then be continued: the ab genomes—*Brassica juncea* ($n = 18$), ac—*B. napus* ($n = 19$), and bc—*B. carinata* ($n = 17$). Species whose genomes fall into the same group or groups cross readily and are, in general, fertile.

The situation has led to proposals (176, 229) for a simplified taxonomic classification of the species considered here. The work reviewed emphasizes the value of combining information from diverse biological disciplines for the solution of a common problem.

LITERATURE CITED

1. Akhtar, A. R. Studies in Indian Brassicae. I. Sterility and selective pollen tube growth. Indian Jour. Agr. Sci. **2**: 280–292. 1932.
2. Alam, Z. Cytological studies of some Indian oleiferous Cruciferae. III. Ann. Bot. **50**: 85–102. 1936.
3. Allgayer, H. Genetische Untersuchungen mit Gartenkohl (*Brassica oleracea*) nach Kreuzungsversuchen von Richard Freudenberg. Zeit. Ind. Abst. u. Vererb. **47**: 191–260. 1928.
4. Anderson, M. E. Fusarium resistance in Wisconsin Hollander cabbage. Jour. Agr. Res. **47**: 639–661. 1933.
5. Attia, M. S. The nature of incompatibility in cabbage. Proc. Am. Soc. Hort. Sci. **56**: 369–371. 1950.
6. ———— and Munger, H. M. Self-incompatibility and the production of hybrid cabbage seed. Proc. Am. Soc. Hort. Sci. **56**: 363–368. 1950.
7. Bailey, L. H. The cultivated Brassicas. Gentes Herb. **1**: 53–108. 1922.
8. ————. The cultivated Brassicas. Gentes Herb. **2**: 211–267. 1930.
9. ————. Certain noteworthy Brassicas. Gentes Herb. **4**: 319–330. 1940.
10. ————. Manual of cultivated plants. 1116 p. (Revised). 1949.
11. Bain, D. C. Reaction of *Brassica* seedlings to black rot. Phytopath. **42**: 497–500. 1952.
12. ————. Blackrot resistance in cabbage. Phytopath. **44**: 331. 1954. [Abst.]
13. Barker, E. E., and Cohen, R. H. Variability in the radish. Jour. Hered. **9**: 357–361. 1918.
14. Becker, Th. Siebenjährige blutenbiologische Studien an den Cruciferen *Brassica napus* L., *Brassica rapa* L., *Brassica oleracea* L., *Raphanus* L. und *Sinapis* L. Zeits. Pflanzenzücht. **30**: 222–240. 1950.
15. Bishop, C. J. The genetical basis of sterility in tetraploid broccoli. Genetics **32**: 79. 1947. [Abst.]

16. BLANK, L. M. Fusarium resistance in Wisconsin All Seasons cabbage. Jour. Agr. Res. **55**: 497–510. 1937.
17. ———— and WALKER, J. C. Inheritance of Fusarium resistance in brussels sprouts and kohlrabi. Jour. Agr. Res. **46**: 1015–1022. 1933.
18. BOSWELL, V. R. A study of some environmental factors influencing the shooting to seed of wintered-over cabbage. Proc. Am. Soc. Hort. Sci. **22**: 380–393. 1925.
19. ————. Studies of premature flower formation in wintered-over cabbage. Md. Agr. Exp. Sta., Bull. 313. 1929.
20. ————. Our vegetable travellers. Nat. Geog. **96**: 145–217. 1949.
21. BRANION, H. D., ROBERTS, J. S., CAMERON, C. R., and MCCREADY, A. M. The ascorbic acid content of cabbage. Jour. Am. Diet. Ass'n. **24**: 101–104. 1948.
22. BRENKEY, E. P., and CARLSON, E. C. Control of the cabbage aphid (*Brevicoryne brassicae*) in cabbage beds and seed fields. Wash. Agr. Exp. Sta., Bull. 455: 38. Ann. Rep. 1944.
23. BRUNE, W. Observations on compatibility within the genus *Brassica*. Rev. Ceres [Brazil] **8**: 158–172. 1949.
24. BURRELL, R. C., BROWN, H. D., and EBRIGHT, V. R. Ascorbic acid content of cabbage as influenced by variety, season, and soil fertility. Food Res. **51**: 247–252. 1940.
25. CALDER, R. A. Interpollination of Brassicas. Its significance in relation to seed-production. New Zeal. Jour. Agr. **55**: 299–308. 1937.
26. Calif. Agr. Exp. Sta., Ann. Rep. **1929**: 104. 1929.
27. CANDOLLE, ALPHONSE DE. Origin of cultivated plants. 1884.
28. CATCHESIDE, D. G. The chromosomal relationships in the swede and turnip groups of *Brassica*. Ann. Bot. **48**: 601–633. 1934.
29. ————. Secondary pairing in *Brassica oleracea*. Cytologia, Fujii Jub. Vol.: 366–378. 1937.
30. CHOPINET, R. Sur quelques hibrides expérimentelle interspécifique et intergénérique chez les crucifères. Compt. Rend. Acad. Sci. [Paris] **215**: 545–547. 1942.
31. ————. Nos choux cultivés: leurs relations genetiques et la nomenclature moderne. Rev. Hort. Paris **30**: 435–440. 1947.
32. CRANE, M. B. The origin and relationships of the *Brassica* crops. Jour. Roy. Hort. Soc. **68**: 172–174. 1943.
33. CRESCINI, FRANCESCO. Il "Rafanobrassica" (*Raphanus sativus* × *Brassica oleracea*). Italia Agric. **79**(5): 253–258. 1942.
34. DANIEL, LUCIEN. Sur deux greffes nouvelles. Compt. Rend. Acad. Sci. [Paris] **184**: 1084–1085. 1927.
35. DARK, S. O. S. The development of the flowers from the curd of broccoli (*Brassica oleracea botrytis*). Ann. Bot. (N.S.) **2**: 751–752. 1938.
36. DAVEY, V. McM. Colour inheritance in swedes and turnips and its bearing on the identification of commercial stocks. Scot. Jour. Agr. **14**: 303–316. 1913.
37. ————. Inheritance of colour in *Brassica napus*. Jour. Genet. **25**: 183–190. 1932.
38. ————. Hybridization in Brassicae and the occasional contamination of seed stocks. Ann. Appl. Biol. **26**: 634–636. 1939.
39. DAVIES, D. W., GRIFFITH, MOSES, and EVANS, GWILYM. "Finger and toe" experiments in Mid-Wales, involving the use of resistant varieties of swedes Welsh Jour. Agr. **4**: 295–303. 1928.
40. DAVIES, W. M. The "many necked" condition of swedes in relation to varietal and manurial trials. Welsh Jour. Agr. **7**: 319–332. 1931.
41. DETJEN, L. R. A preliminary report on cabbage breeding. Proc. Am. Soc. Hort. Sci. **23**: 325–332. 1926.

42. ————. Sterility in the common cabbage (*Brassica oleracea* L.). Mem. Hort. Soc. New York **3**: 277–280. 1926.
43. ———— and McCUE, C. A. Cabbage characters and their heredity. Del. Agr. Exp. Stat., Bull. 180. 1933.
44. DOOLITTLE, S. P. Vegetable disease investigations in the United States Department of Agriculture, 1885–1950. U. S. Dept. Agr., Plant Dis. Rep., Suppl. **195**: 398–412. 1950.
45. EDDINS, A. H. Cabbage diseases other than downy mildew and Alternaria leafspot. Fla. Agr. Exp. Sta., Ann. Rep. **1950**: 116–117. 1950.
46. EDWARDS, S. F. Cabbage resistance to black rot. Ont. Agr. Col., Ann. Rep. (1907) **33**: 134. 1908.
47. EVANS, A. C. Physiological relationships between insects and their host plants. I. The effect of the chemical composition of the plant on reproduction and production of winged forms in *Brevicoryne brassicae* L. (Aphididae). Ann. Appl. Biol. **25**: 558–572. 1938.
48. FAIRCHILD, DAVID. The world was my garden. 1938. [p. 165, 407].
49. FEDORINCHIK, N. S. [Investigation on the determination of the injuriousness of the *Plasmodiophóra brassicae* and development of immune varieties of cabbage]. Vestnik Zashch. Rast. [Plant Prot]. Leningrad **2**: 87–95. 1935. [Russia with Engl. summ].
50. FINDLAY, W. M. A disease-resisting turnip. Scot. Jour. Agr. **14**: 173–183. 1931.
51. FOSTER, H. H. Reaction of species and varieties of Cruciferae to artificial inoculation of cabbage downy mildew. Phytopath. **37**: 433. 1947. [Abst.]
52. ———— and PINCKARD, J. A. Resistance to rust by cabbage tested at Crystal Spring. Miss. Farm Res. **7**(11) : 7. 1944.
53. FOSTER, R. E., and WALKER, J. C. Improvement of ascorbic acid content in yellows-resistant cabbage. Phytopath. **36**: 398. 1946. [Abst.]
54. FRANDSEN, K. J. The experimental formation of *Brassica napus* L. var. *oleifera* D.C. and *Brassica carinata* Braun. Dansk. Bot. Arkiv. **12**(7) : 1–16. 1947.
55. FRANDSEN, H. N., and WINGE, O. *Brassica napocampestris*, a new constant amphidiploid species hybrid. Hereditas **16**: 212–218. 1932.
56. FROST, H. B. Heterosis and dominance of size factors in *Raphanus*. Genetics **8**: 116–153. 1923.
57. FUKUSHIMA, E. Preliminary report on *Brassica–Raphanus* hybrids. Proc. Imp. Acad. Tokyo **5**: 48–50. 1929.
58. ————. On the F_1 hybrid between *Brassica carinata* and the radish. Jap. Jour. Genet. **18**: 202–203. 1942.
59. ————. Cytogenetic studies on *Brassica* and *Raphanus*. I. Studies on the intergeneric F_1 hybrids between *Brassica* and *Raphanus*. Jour. Dept. Agr. Kyushu Univ. **7**: 282–400. 1945.
60. FURTADO, C. X., and HOLTTUM, R. E. The Chinese mustards and cabbages grown in Singapore. M.A.H.A. Mag. [Kuala Lumpur] **10**: 47–51. 1940.
61. GALLASTEGUI, CRUZ. Numero de cromosomas en algunas especies del genero *Brassica*. Bol. R. Soc. Espan. Hist. Nat. **26**: 185–191. 1926.
62. GANTE, TH. Hernieresistenz bei Weisskohl. I. Zeits. Pflanzenzücht. **30**: 188–197. 1951.
63. GATES, R. R. Wild cabbages and the effects of cultivation. Jour. Genet. **51**: 363–372. 1953.
64. GERRETSEN, F. C., and HAAGSMA, NETTY. Occurrence of antifungal substances in *Brassica rapa*, *Brassica oleracea* and *Beta vulgaris*. Nature **168**: 659. 1951.
65. GOULD, S., TRESSLER, D. K., and KING, C. G. Vitamin C content of vegetables. V. Cabbage. Food Res. **1**: 472. 1936.

66. GRAVATT, A. A radish-cabbage hybrid. Jour. Hered. **5**: 269–272. 1914.
67. GREBINSKAIA, M. I. [The anatomy of the amphidiploid *Raphanobrassica* and its parent]. Bot. Zhurn. SSSR [Jour. Bot. URSS] **23**: 106–121. 1938. [Russian with Eng. summ.]
68. HAGA, T. Relationship of genom to secondary pairing in *Brassica*. Jap. Jour. Genet. **13**: 277–284. 1938.
69. HALLQVIST, C. Brassicakreuzungen. Bot. Not. **1915**: 97–112. 1915.
70. ————. Ein neuer Fall von Dimerie bei *Brassica napus*. Bot. Not. **1916**: 39–42. 1916.
71. HALLSWORTH, E. G., and LEWIS, V. M. Ascorbic acid in cabbages. Emp. Jour. Exp. Agr. **17**: 28–36. 1949.
72. HARRISON, P. K., and BRUBAKER, R. W. The relative abundance of cabbage caterpillars on cole crops grown under similar conditions. Jour. Econ. Ent. **36**: 589–592. 1943.
73. HARVEY, R. B. Varietal differences in the resistance of cabbage and lettuce to low temperature. Ecology **3**: 134–139. 1923.
74. HENDRICK, J. The prevention of finger-and-toe in turnips. Liming and a disease resistant variety. Trans. Highl. Agr. Soc. Scot. **44**: 52–63. 1932.
75. HENSLOW, G. The history of the cabbage tribe. Jour. Roy. Hort. Soc. **34**: 15–23. 1908.
76. HERRMANN, F. Ueber die Vererbung des Kopf- und Knollenbildung bei Kohl und Kohlrabi. Gartenwelt. **25**: 146–148. 1921.
77. HOUGAS, R. W., RIEMAN, G. H., and STOKES, G. W. Resistance to white rust in horseradish seedlings. Phytopath. **42**: 109–110. 1952.
78. HOWARD, H. W. The chromosome number of the swede, *Brassica napus* L. Jour. Genet. **35**: 383–386. 1938.
79. ————. The fertility of amphidiploids from the cross *Raphanus sativus* × *Brassica oleracea*. Jour. Genet. **36**: 239–273. 1938.
80. ————. The cytology of autotetraploid kale, *Brassica oleracea*. Cytologia **10**: 77–87. 1939.
81. ————. The size of seeds in diploid and autotetraploid *Brassica oleracea* L. Jour. Genet. **38**: 325–340. 1939.
82. ————. The nomenclature of *Brassica* species. Curr. Sci. **9**: 494–495. 1940.
83. ————. The effect of polyploidy and hybridity on seed size in crosses between *Brassica chinensis*, *B. carinata*, amphidiploid *B. chinensis-carinata* and autotetraploid *B. chinensis*. Jour. Genet. **43**: 105–119. 1942.
84. ————. Self-incompatibility in polyploid forms of *Brassica* and *Raphanus*. Nature **149**: 302–303. 1942.
85. ————. Autotetraploid green watercress. Jour. Hort. Sci. **27**: 273–277. 1952.
86. IWASA, S. [Studies on artificial triploid and hexaploid *Brassica* types having the three genomes abc.] [Sci. Bul. Fact. Agr. Kyushu Univ.] **13**: 90–99. 1951. [Japanese] [Plant Breed. Abst. **24**: 1202] [Original not seen.]
87. JARETZKY, R. Beziehungen zwischen Chromosomenzahl und Systematik bei den Cruciferen. Jahrb. Wiss. Bot. **4**: 485–527. 1932.
88. JONES, L. R. Disease resistance in cabbage. Proc. Nat. Acad. Sci. **4**: 42–46. 1918.
89. ———— and GILMAN, J. C. The control of cabbage yellows through disease resistance. Wisc. Agr. Exp. Sta., Res. Bull. 38. 1915.
90. ————, WALKER, J. C., and MONTEITH, JOHN, JR. Fusarium resistant cabbage: progress with second early varieties. Jour. Agr. Res. **30**: 1027–1034. 1925.
91. KAJANUS, B. Genetische Studien an *Brassica*. Zeit. Ind. Abst. u. Vererb. **6**: 217–237. 1912.

92. ————. Ueber die Vererbungsweise gewisser Merkmale der *Beta*- und *Brassica*-Ruben. II. *Brassica*. Zeits. Pflanzenzücht. **1**: 419–463. 1913.
93. ————. Über Bastardierungen zwischen *Brassica napus* L. und *Brassica rapa* L. Zeits. Pflanzenzücht. **5**: 265–322. 1917.
94. KAKIZAKI, Y. Self-sterility in the Chinese cabbage. Jour. Hered. **13**: 374–376. 1922.
95. ————. A preliminary report of crossing experiments with cruciferous plants, with special reference to sexual compatibility and matroclinous hybrids. Jap. Jour. Genet. **3**: 49–82. 1925.
96. ————. An instance of radish-cabbage hybrids. Jour. Sci. Agr. Soc. Japan **298**: 438–446. 1927.
97. ————. A dominant white-flowered mutant of *Brassica oleracea* L. Jap. Jour. Genet. **6**: 55–60. 1930.
98. ————. Studies on the genetics and physiology of self- and cross-incompatibility in the common cabbage (*Brassica oleracea* L. var. *capitata* L.). Jap. Jour. Bot. **5**: 133–208. 1930.
99. ———— and KASAI, TADAYUKI. Bud pollination in cabbage and radish. Jour. Hered. **24**: 359–360. 1933.
100. KARPECHENKO, G. D. [The number of chromosomes and the genetic correlation of cultivated cruciferae]. [Bul. Appl. Bot., Genet. & Pl. Breed]. **13**: 3–14. 1922. [Russian]
101. ————. Hybrids of ♀ *Raphanus sativus* L. × ♂ *Brassica oleracea* L. Jour. Genet. **14**: 375–396. 1924.
102. ————. The production of polyploid gametes in hybrids. Hereditas **9**: 349–368. 1927.
103. ————. [Polyploid hybrids of *Raphanus sativus* L. × *Brassica oleracea* L.] [Bull. Appl. Bot. & Plant-Breed.] **17**(3): 305–408. 1927. [Russian with Eng. summ.]
104. ————. Polyploid hybrids of *Raphanus sativus* L. × *Brassica oleracea* L. Zeit. Ind. Abst. u. Vererb. **48**: 1–85. 1928.
105. ————. [A contribution to the synthesis of a constant hybrid of three species]. Proc. U.S.S.R. Congr. Genet. **2**: 277–294. 1929. [Russian with Engl. summ.]
106. ————. [Increasing the crossability of a species by doubling its chromosome number.] [Bull. Appl. Bot., Genet. and Pl. Breed. Ser. II.] **7**: 37–51. 1937. [Russian with Eng. summ.]
107. ————. [Experimental production of tetraploid hybrids, *Brassica oleracea* L. × *B. carinata* Al. Braun.] [Bull. Appl. Bot., Genet. and Pl. Breed. Ser. II.] **7**: 53–68. 1937. [Russian with Eng. summ.]
108. ————. [Reciprocal hybrids between Raphanobrassica and tetraploid cabbage.] [Bull. Appl. Bot., Genet. and Pl. Breed. Ser. II.] **7**: 447–453. 1937. [Russian with Eng. summ.]
109. ———— and BOGDANOVA, E. N. [A fertile tetraploid hybrid *Brassica oleracea* L. × *Brassica chinensis* L., experimentally produced.] [Bull. Appl. Bot. Leningrad Ser. II.] **7**: 455–464. 1937.
110. KRISTOFFERSON, K. B. Untersuchungen über die F_1 und F_2 Generation von einem spontanen Bastard zwischen Weisskraut und Grünkohl. Sveriges Utsad. Tidsk. **1921**: 31–52. 1921. [German summ.]
111. ————. Contributions to the genetics of *Brassica oleracea*. Hereditas **5**: 297–364. 1924.
112. ————. Contributions to the genetics of *Brassica oleracea*. II. Hereditas **9**: 343–348. 1927.
113. KONDO, N. [A new *Raphanobrassica* from the cross 4*x* *Raphanus sativus* L. × 4*x* *Brassica oleracea* L.] Jap. Jour. Genet. **18**: 126–130. 1942. [Japanese.] [Plant Breed. Abst. **21**: 2196.] [Original not seen.]

114. KOTOWSKI, F. Effect of self fertilization in cabbage and onion. Mem. Hort. Soc. New York **3**: 281–284. 1926.
115. KRICKL, M. Zur Züchtung von frestwiderstandsfaehigen und nichtholzig werden den fruehn Kohlrabi. Gartenbauwiss. **18**: 185–203. 1944.
116. ————. Genügen die derzeitigen Werteigenschaften der Radieschen? Saatgutwirtschaft [Stuttgart] **5**: 63–64. 1953.
117. KVASNIKOV, B. V., OSNICKAJA, E. A., and DEMSENKO, A. I. [The resistance to club root of cabbage varieties]. [Fruit Vegetable Gardens] **1950**: 51–53. 1950.
118. KWAN, C. C. Inheritance of some plant characters in cabbage, *Brassica oleraceae* var. *capitata*. Jour. Agr. Ass'n. China No. 126–127: 81–127. 1934.
119. LAMPRECHT, H., and HERTZMAN, N. [Immuna II, a new variety of turnip, resistant to finger and toe]. Agri Hort. Genet. **1**: 31–33. 1943. [Swedish with Engl. summ.]
120. LARSON, R. H., and WALKER, J. C. A mosaic disease of cabbage. Jour. Agr. Res. **59**: 367–392. 1939.
121. LEBEAU, F. J., and WALKER, J. C. Turnip mosaic viruses. Jour. Agr. Res. **70**: 347–364. 1945.
122. LEE, S. H. The effect of bud pollination on fertility and F_1 fruit characters of some Chinese Brassicas. Proc. Am. Soc. Hort. Sci. **52**: 435–440. 1948.
123. LING, L., and YANG, J. Y. A mosaic of rape and other cultivated crucifers in China. Phytopath. **30**: 338–342. 1940.
124. LOBB, W. R. Resistant type of rape for areas infected with club root. New Zeal. Jour. Agr. **82**: 65–66. 1951.
125. LONGREE, KARLA, and FENTON, FAITH. Objective and subjective studies on factors affecting toughness and stringiness of kale (*Brassica oleracea acephala*.) Food Res. **15**: 471–489. 1950.
126. MAEDA, T., and SASAKI, T. Chromosome behavior in the pollen mother cells of "Shogoindaikon" and "Nerimadaikon" the horticultural varieties of *Raphanus sativus* L. Jap. Jour. Genet. **10**: 78–83. 1934. [Japanese with Eng. summ.]
127. MAGRUDER, R. A new color type in cabbage. Science **85**: 427–428. 1937.
128. ————. Improvement in the leafy cruciferous vegetables. U. S. Dept. Agr., Yrbk. **1937**: 289–299. 1937.
129. ———— and MYERS, C. H. The inheritance of some plant colors in cabbage. Jour. Agr. Res. **47**: 233–248. 1933.
130. MALINOWSKI, E. On the inheritance of some characters in radishes. Compt. Rend. Soc. Sci. Varsovie **9**: 757–776. 1916. [Polish and English].
131. ————. [On the hybrids of cabbage with curly-leaved kale]. Mem. Inst. Genet. Ecole Super. Agr. Varsovie **1**: 1–14. 1921. [Polish] [Reviewed in Zeits. Pflanzenzücht. **9**: 152.] [Original not seen].
132. ————. Quelques observations sur les hybrides du genre *Brassica*. Mem. Inst. Genet. Ecole Super. Agr. Varsovie **2**: 145–162. 1924. [Polish with French summ.]
133. ————. Kilka obserwacji nad mieszancami rodzaju *Brassica*. Pam. Zakladu. Genet. Szkoly Glownej Gosp. Wiejskiego w Warszawie 2: 145–162. 1924. Cited by H. Matsuura. A Bibliographical Monograph on Plant Genetics. 1933.
134. ————. Genetics of *Brassica*. Bib. Genet. **5**: 1–26. 1929.
135. MANTON, IRENE. Introduction to the cytology of Cruciferae. Ann. Bot. **46**: 509–556. 1932.

136. ————. The cytological history of watercress (*Nasturtium officinale* R. Br.). Zeits. Ind. u. Abst. Vereb. **69**: 132–157. 1935.
137. MELHUS, I. E., ERWIN, A. T., and VAN HALTERN, F. Cabbage yellows caused by *Fusarium conglutinans* in Iowa. Iowa Agr. Exp. Sta., Bull. 235. 1926.
138. ———— and PORTER, D. R. The use of selection and selfing in improving Iacope cabbage. Phytopath. **18**: 142. 1928. [Abst.]
139. MILLER, J. C. A study of some factors affecting seed-stalk development in cabbage. N. Y. (Cornell) Agr. Exp. Sta., Bull. 488. 1929.
140. ————. Some factors associated with puffy-headed cabbage. Proc. Am. Soc. Hort. Sci. **34**: 495–497. 1937.
141. MIZUSHIMA, U. Karyogenetic studies of species and genus hybrids in the tribe *Brassiceae* of *Cruciferae*. Tohoku Jour. Agr. Res. **1**: 1–14. 1950.
142. ————. On several artificial allopolyploids obtained in the tribe *Brassiceae* of *Cruciferae*. Tohoku Jour. Agr. Res. **1**: 15–27. 1950.
143. ———— and KATSUO, K. A new case of incompatibility in *Brassica oleracea* L. Jap. Jour. Breed. **2**: 121–125. 1953. [Japanese with Eng. summ.]
144. MOHAMMAD, A., and SIKKA, S. M. Pseudogamy in genus *Brassica*. Curr. Sci. **9**: 280–282. 1940.
145. ————, SINGH, R. D., and ALAM, Z. Some breeding investigations on toria (*Brassica napus* L. var. *dichotoma* Prain) and sarson (*Brassica campestris* L. var. *sarson* Prain). Indian Jour. Agr. Sci. **1**: 109–136. 1931.
146. MOLDENHAWER, K. Über die Gattungskreuzungen *Raphanus* × *Brassica*. Mem. Inst. Genet. Ecole Super. Agr. Varsovie **2**: 191–196. 1924.
147. ————. [Studies of a hybrid of *Raphanus* with *Brassica*.] Bull. Internat. Acad. Polonaise Sci. et Let. Ser. B. Sci. Nat. **1925**: 537–560. 1925. [Biol. Abst. **2**: 426.] [Original not seen]
148. ————. Recherches sur certains croisements interessants du genre *Brassica*. Bull. Int. Acad. Polonaise Sci. et Lett. Cl. Sci. Math., et Nat. Ser. B: Sci. Nat. **1927**: 1049–1071. 1928.
149. MORINAGA, T. Interspecific hybridization in Brassica. II. The cytology of F_1 hybrids of *B. cernua* and various other species with 10 chromosomes. Jap. Jour. Bot. **4**: 227–289. 1929.
150. ————. Interspecific hybridization in *Brassica*. III. The cytology of F_1 hybrid of *B. cernua* and *B. napella*. Jour. Dept. Agr. Kyushu Imp. Univ. **2**: 199–206. 1929.
151. ————. Interspecific hybridization in *Brassica*. IV. The cytology of F_1 hybrids of *B. carinata* and some other species with 10 chromosomes. Cytologia **3**: 77–83. 1931.
152. ————. Interspecific hybridization in *Brassica*. V. The cytology of F_1 hybrid of *B. carinata* and *B. alboglabra*. Jap. Jour. Bot. **6**: 467–475. 1933.
153. ————. Interspecific hybridization in *Brassica*. VI. The cytology of F_1 hybrids of *B. juncea* and *B. nigra*. Cytologia **6**: 62–67. 1934.
154. ———— and FUKUSHIMA, E. Another new chromosome number in *Brassica*. Bot. Mag. Tokyo **44**: 373–374. 1930.
155. ———— and ————. Kariological studies on a spontaneous haploid mutant of *Brassica napella*. Cytologia **4**: 457–460. 1933.
156. ———— and KURIYAMA, H. On the autopolyploids of the rape. Cytologia, Fujii Jub. Vol.: 967–969. 1937.
157. MORRIS, L. E. Pollen germination in *Brassica chinensis* × *Raphanus sativus* F_1 hybrids. Jour. Genet. **33**: 435–441. 1936.
158. ———— and RICHHARIA, R. H. A triploid radish × turnip hybrid and some of its progeny. Jour. Genet. **34**: 275–286. 1937.

159. MURPHY, E. F. The ascorbic acid content of different varieties of Maine-grown tomatoes and cabbages as influenced by locality, season and stage of maturity. Jour. Agr. Res. **64**: 483–502. 1942.
160. MUSIL, ALBINA F. Distinguishing the species of *Brassica* by their seed. U. S. Dept. Agr., Misc. Pub. 643. 1948.
161. NAGAI, K., and SASAOKA, T. The number of chromosomes in the cultivated *Brassica*. Jap. Jour. Genet. **5**: 151–158. 1930. [Japanese with Eng. summ.]
162. ———— and ————. [Chromosome number of crop varieties belonging to Cruciferae. Additional report.] Jour. Okitsu Hort. Sci. No. 25: 76-77. 1930. [Japanese] Cited by H. W. Howard. Jour. Genet. **35**: 383–386. 1938.
163. Nat. Inst. Agr. Bot. Cambridge. Cross fertilization in Brassicas. Jour. Min. Agr. (Gr. Brit.) **49**(1): 116–117. 1942.
164. NATTI, J. J. Cabbage viruses in New York state. N. Y. Agr. Exp. Sta., Farm Res. **18**(4): 7. 1952.
165. NELSON, A. Fertility in the genus *Brassica*. Jour. Genet. **18**: 110–135. 1926.
166. NETROUFAL, F. Zytologische Studien über die Kulturrassen von *Brassica oleracea*. Osterreich. Bot. Zeits. **76**: 101–115. 1927.
167. NEWCOMER, E. H. An F_2 colchicine-induced tetraploid cabbage and some comparisons with its diploid progenitor. Jour. Elisha Mitchell Sci. Soc. **59**: 69–72. 1943.
168. NISHIYAMA, I. [Breeding cold-resistant *Raphanus sativus* by the doubling of chromosome number.] Bot. and Zool. **10**: 57–58. 1942. [Plant Breed. Abst. **21**: 688.] [Original not seen].
169. NOGUCHI, Y. Cytological studies on a case of pseudogamy in the genus *Brassica*. Proc. Imp. Acad. [Tokyo] **4**: 617–619. 1928.
170. NYLUND, R. E. Ascorbic acid content of twenty-five varieties of the rutabaga. Proc. Am. Soc. Hort. Sci. **54**: 367–372. 1949.
171. ODLAND, M. L., and NOLL, C. J. The utilization of cross-compatibility and self-incompatibility in the production of F_1 hybrid cabbage. Proc. Am. Soc. Hort. Sci. **55**: 390–402. 1950.
172. OKUNO, S. [The genetics of root color in the radish.] Jap. Jour. Genet. **19**: 99–100. 1943. [Japanese] [Plant Breed. Abst. **21**: 3054. 1951.] [Original not seen].
173. OLSSON, GÖSTA. [The crossing ability between different species of *Brassica*.] Sveriges Utsadosforen. Tidskr. **59**: 193–195. 1949. [Biol. Abst. **24**: 22498]. [Original not seen].
174. ————. Crosses between *Brassica napus* L. and Japanese *Brassica napella* Chaix. Hereditas **40**: 249–252. 1954. [Abst.]
175. ————. Crosses within the *campestris* group of the genus *Brassica*. Hereditas **40**: 398–418. 1954.
176. PEARSON, O. H. A suggested classification of the genus *Brassica*. Proc. Am. Soc. Hort. Sci. **25**: 105–110. 1928.
177. ————. A dominant white flower color in *Brassica oleracea* L. Am. Nat. **63**: 561–565. 1929.
178. ————. Further observations on the type of sterility in *Brassica oleracea* var. *capitata* L. Proc. Am. Soc. Hort. Sci. **27**: 337–342. 1930.
179. ————. Influence of inbreeding upon the season of maturity in cabbage. Proc. Am. Soc. Hort. Sci **28**: 359–366. 1931.
180. ————. Incompatibility in broccoli and the production of seed under cages. Proc. Am. Soc. Hort. Sci. **29**: 468–471. 1933.
181. ————. Study of the life history of *Brassica oleracea*. Bot. Gaz. **94**: 534–550. 1933.
182. ————. Dominance of certain quality characters in cabbage. Proc. Am. Soc. Hort. Sci. **31**: 169–176. 1934.

183. PEASE, M. S. Genetic studies in *Brassica oleracea*. Jour. Genet. **16**: 363–385. 1926.
184. ————. Genetic studies in *Brassica*. II. The kohlrabi. Jour. Genet. **17**: 253–267. 1927.
185. PIECH, K., and MOLDENHAWER, K. Zytologische Untersuchungen an Bastarden zwischen *Raphanus* und *Brassica*. Bull. Int. Acad. Polonaise Sci. et Lettr. Cl. Sci. Math. et Nat. **1927**: 23–38. 1927.
186. POLITIS, J. Sur des gènes produisant de l'anthocyane dans les plantulas de *Raphanus sativus* et d'autres Crucifères. Compt. Rend. Acad. Sci. [Paris] **225**: 256–257. 1947.
187. POOLE, C. F., GRIMBALL, P. C., and KANAPAUX, M. S. Factors affecting the ascorbic acid content of cabbage lines. Jour. Agr. Res. **68**: 325–329. 1944.
188. POUND, G. S. Reaction of cabbage varieties to mosaic viruses. Jour. Agr. Res. **75**: 19–30. 1947.
189. ———— and FOWLER, D. L. Fusarium wilt of radish in Wisconsin. Phytopath. **43**: 277–280. 1953.
190. ———— and WALKER, J. C. Mosaic resistance in cabbage. Phytopath. **41**: 1083–1090. 1951.
191. PRICE, H. L. Inheritance in cabbage hybrids. Va. Agr. Exp. Sta., Ann. Rep. **1911/1912**: 240–257. 1912.
192. RAGIONIERI, A. *Brassica* crosses. Gard. Chron. **68**: 60. 1920.
193. RAMANUJAM, S. An apetalous mutation in turnip (*Brassica campestris* L.). Nature **145**: 552–553. 1940.
194. ————. Autotriploidy in toria (*Brassica campestris* L.). Curr. Sci. **9**: 325–326. 1940.
195. RAO, L. N. Flowering branches from the curd of *Brassica oleraceae* L. var. *botrytis* D.C. Curr. Sci. **7**: 237–238. 1938.
196. RASMUSSON, J. Results from a cross cabbage × savoy cabbage. Hereditas **16**: 241–248. 1932.
197. REICHELT, K. Die Bekämpfung der Kohlmade. Möllers Deut. Gärtner-Zeit. **41**: 59–60. 1926.
198. REINKING, O. A., and GLOYER, W. O. Most cauliflower varieties resistant to cabbage yellows. N. Y. Agr. Exp. Sta., Farm Res. **6**(4): 8. 1940.
199. REITBERGER, A. Über polyploidie Ruhekerne bei Cruciferen. Naturwiss. **36**: 380. 1949.
200. ————. Chromozentrenuntersuchungen. I. Mitteilung. Über die Struktur junger Ruhekerne verscheidener Valenz bei vier Kruziferarten. Chromosoma **4**: 205–221. 1951.
201. RICHHARIA, R. H. Cytological investigation of *Raphanus sativus*, *Brassica oleracea*, and their F_1 and F_2 hybrids. Jour. Genet. **34**: 19–44. 1937.
202. ————. Cytological investigations of 10-chromosome species of *Brassica* and their F_1 hybrids. Jour. Genet. **34**: 45–55. 1937.
203. ————. Investigation on F_1 and F_2 hybrids between *Brassica carinata* and *Raphanus sativus*. Jour. Indian Bot. Soc. **16**: 137–144. 1937.
204. ROCHLIN, E. Zur Frage der Widerstandsfähigkeit der Cruciferen gegen die Kohlhernie (*Plasmodiophora brassicae* Wor.). Phytopath. Zeits. **5**: 381–406. 1933.
205. ROEMER, W. Fruchtbarkeits- und Vererbungsstudien bei Brassica-artkreuzungen. Zeits. Pflanzenzücht. **20**: 377–416. 1935.
206. RONEY, J. N. Truck crop insect investigations. Tex. Agr. Exp. Sta., Ann. Rep. **46**: 50. 1933.
207. SAMSON, S. Le *Brassica oleracea*. Quelques caractères héréditaires du *Brassica oleracea*. Rev. Inst. Agr. d'Oka. **4**: 92–95. 1930.

208. ————. La genetique du *Brassica oleracea*. Rev. Inst. Agr. d'Oka. **4**: 121–122. 1930.
209. SASAOKA, T. On the pollen-tube growth in some species of *Brassica*. Imp. Hort. Exp. Sta., Okitu, Japan, Res. Bull. 11. 1928.
210. ————. Karyological observations in different interspecific hybrids of *Brassica*. Jap. Jour. Genet. **6**: 20–32. 1930.
211. SCHEFFER, R. P. Anthracnose leafspot of crucifers. N. C. Agr. Exp. Sta., Tech. Bull. 92. 1950.
212. SEARS, E. R. Cytological phenomena connected with self-sterility in the flowering plants. Genetics **22**: 130–181. 1937.
213. SHCHAVINSKAYA, S. A. Tetraploid cabbage obtained by means of regeneration. Bull. Appl. Bot., Genet., and Pl. Breed. Ser. II **7**: 13–36. 1937. [Russian with Eng. summ.]
214. ————. Octoploid cabbage experimentally obtained. Bull. Appl. Bot., Genet., and Pl. Breed. II. **7**: 69–77. 1937. [Russian with Eng. summ.]
215. ————. Elimination of radish chromosomes and conditions necessary for their functioning in crosses of cabbage and its polyploid forms with radish and radish-cabbage hybrids. Bull. Appl. Bot., Genet., and Pl. Breed. Ser. II. **7**: 79–91. 1937. [Russian with Eng. summ.]
216. SHIMOTOMAI, N. A karyological study of *Brassica* I. Bot. Mag. [Tokyo] **39**: 122–127. 1925.
217. SHISA, M., and HAZU, G. [Studies on resistance to snow in *Brassica*. I. Varietal differences in physiological characters associated with resistance to snow.] Jour. Hort. Assn. Japan **20**: 98–104. 1951. [Japanese] [Plant Breed. Abst. **23**: 1531. 1953.] [Original not seen.]
218. SIKKA, S. M. Cytogenetics of *Brassica* hybrids and species. Jour. Genet. **40**: 441–509. 1940.
219. SIMONET, M. Sur l'obtention de plantes géantes et polyploïdes, après application de colchicine. Compt. Rend. Acad. Agr. France **24**: 846–850. 1938.
220. ———— and CHOPINET, R. Sur la création de variétés nouvelles tétraploïdes à grandes fleurs après traitement chimique. Rev. Hort. (n.s.) **18**: 146–152. 1942.
221. SINSKAIA, E. Genetic systematic studies on cultivated Brassica. Bull. Appl. Bot. & Plant-Breed. **17**(1): 3–166. 1927. [Russian with Eng. summ.]
222. SINSKAIA, E. N. The oleiferous plants and root crops of the family Cruciferae. Bull. Appl. Bot., Genet. and Pl. Breed. **19**(3): 1–648. 1928. [Russian with Eng. summ.]
223. SISA, M. A list of the chromosome number in vegetable crops. Jap. Jour. Genet. **5**: 88–95. 1929.
224. SMITH, F. G., and WALKER, J. C. Relation of environmental and hereditary factors to ascorbic acid in cabbage. Am. Jour. Bot. **33**: 120. 1946.
225. STERLING, J. D. E. The inheritance of flesh colour and clubroot reaction in swedes. Sci. Agr. **31**: 253–268. 1951.
226. STOUT, A. B. Cyclic manifestation of sterility in *Brassica pekinensis* and *B. chinensis*. Bot. Gaz. **73**: 110–132. 1922.
227. ————. Pollen tube behavior in *Brassica pekinensis* with reference to self incompatibility in fertilization. Am. Jour. Bot. **18**: 686–695. 1931.
228. STURTEVANT, E. L. Sturtevant's notes on edible plants. (U. P. Hedrick, Ed.) N. Y. Agr. Exp. Sta., Twenty-seventh Ann. Rep. Vol. 2: 1–686. 1919.

229. Sun, V. G. The evaluation of taxonomic characters of the cultivated *Brassica* with a key to species and varieties. II. The key. Bull. Torrey Bot. Club. **73**: 370–377. 1946.
230. Sutaria, R. N. Microsporogenesis in *Raphanus sativus* L. (the Indian radish). Jour. Indian Bot. Soc. **9**: 253–256. 1930.
231. Sutton, A. W. *Brassica* crosses. Jour. Linn. Soc. (Botany) **38**: 337–349. 1908.
232. Sutton, E. P. F. Inheritance of "bolting" in cabbage. Jour. Hered. **15**: 257–260. 1924.
233. Sylven, N. Kreuzungsstudien beim Raps (*Brassica napus olifera*). Hereditas **9**: 380–390. 1927. [English summ.]
234. Tandon, S. L. Colchicine-induced polyploidy in *Brassica oleracea* var. *Botrytis* L. Sci. & Cult. **16**: 483–484. 1951.
235. Tatebe, T. [Inheritance of root color in the radish.] Bot. and Zool. **4**: 1385–1392. 1936. [Japanese] [Plant Breed. Abst. **10**: 1142. 1940.] [Original not seen].
236. ———. [Karyological studies on the Japanese radish. (*Raphanus sativus* var. *macropodus* (Lév.) Makino.] Bot. and Zool. **4**: 1893–1900. 1935. [Japanese] [Plant Breed. Abst. **9**: 504. 1939.] [Original not seen.]
237. ———. [Studies on the inheritance of color in the Japanese and Chinese radish.] Bot. and Zool. **5**: 1301–1308. 1937. [Japanese] [Plant Breed. Abst. **12**: 602. 1942.] [Original not seen.]
238. ———. [Studies on the inheritance of root shape in the Japanese and Chinese radish.] Jour. Hort. Assn. Japan **8**: 327–336. 1937. [Japanese] [Plant Breed. Abst. **8**: 1634. 1938.] [Original not seen.]
239. ———. [On inheritance of root color in *Raphanus sativus* Linn.] Jap. Jour. Genet. **14**: 39–50. 1938. [Japanese] [Plant Breed. Abst. **8**: 1633 and **9**: 867. 1939.] [Original not seen.]
240. ———. Studies on the behavior of incompatible pollen in the Japanese radish. Jour. Hort. Assn. Japan **11**: 207–234. 1940. [Japanese with Eng. summ.]
241. ———. Studies on the behavior of incompatible pollen in *Brassica*. IV. *Brassica oleracea* L. var. *capitata* L. and var. *botrytis* L. Jour. Hort. Assn. Japan **20**: 19–26. 1949. [Japanese with Eng. summ.]
242. Tatuno (Tatsuno), S. [On artificial polyploids of the radish. I.] Jap. Jour. Genet. **22**: 31–32. 1947. [Japanese] [Plant Breed. Abst. **22**: 1485. 1952.] [Original not seen.]
243. Tedin, O. [The inheritance of resistance to club root disease (*P. brassicae*) of turnips (*Brassica rapa* v. *rapifera*) in relation to certain morphological characters of the root.] Nord. Jordbr. Forskn. **14**: 324–331. 1932. [English summ.]
244. Terasawa, Y. Konstante amphidiploide *Brassico-Raphanus* Bastarde. Proc. Imp. Acad. Tokyo **8**: 312–314. 1932.
245. ———. Effekt der bastardierung von *Brassico-raphanus* durch *Brassica* und *Raphanus*. Jap. Jour. Genet. **8**: 229–230. 1933. [Japanese] German summ. seen in Jap. Jour. Bot. **7**: 26. 1934.
246. Thomas, R. C., and Magruder, R. Early cabbage resistant to the yellows disease. Ohio Agr. Exp. Sta., Bim. Bull. **13**: 142–144. 1928.
247. Thung, T. H. [Black rot of cabbage]. Landbouw **21**: 259–266. 1949. [Dutch with Eng. summ.]
248. Tokumasu, S. Male-sterility in Japanese radish (*Raphanus sativus* L.) Sci. Bull. Facult. Agr. Kyushu Univ. **13**: 83–89. 1951. [Japanese with Engl. summ.]
249. Tompkins, C. M. A mosaic disease of turnip. Jour. Agr. Res. **57**: 589–602. 1938.

250. ————. A mosaic disease of radish in California. Jour. Agr. Res. **58**: 119–130. 1939.
251. ———— and THOMAS, H. R. A mosaic disease of Chinese cabbage. Jour. Agr. Res. **56**: 541–551. 1938.
252. TROUARD-RIOLLE, YVONNE. Recherches morphologiques et biologiques sur les radis, cultivés. Ann. Sci. Agron. Franç. et Etrang. **31**: 295–322, 346–550. 1914.
253. ————. Hybridation entre une crucifère sauvage et une crucifère cultivée à racine tuberisée. Compt. Rend. Acad. Sci. [Paris] **162**: 511–513. 1916.
254. ————. Les hybrides de *Raphanus*. Rev. Gen. Bot. **32**: 438–447. 1920.
255. TSCHERMAK, E. VON. Ueber den gegenwärtigen Stand der Gemüsezüchtung. Zeits. Pflanzenzücht. **4**: 65–104. 1916.
256. TURESSON, G., and NORDENSKIOLD, H. Chromosome doubling and cross combinations in some cruciferous plants. Lantbr. Hogsk. Ann. [Uppsala] **11**: 201–206. 1943.
257. U, NAGAHARU. Genome-analysis in *Brassica* with special reference to the experimental formation of *B. napus* and peculiar mode of fertilization. Jap. Jour. Bot. **7**: 389–452. 1935.
258. ————, MIDUSIMA, U., and SAITO, K. On diploid and triploid *Brassica–Raphanus* hybrids. Cytologia **8**: 319–326. 1937.
259. ———— and NAGAMATSU, T. On the difference between *Brassica campestris* L. and *B. napus* L. in regard to fertility and natural crossing. Jour. Imp. Agr. Exp. Stat. Nishigahara (Tokyo) **2**: 113–128. 1933. [Japanese with Eng. summ.]
261. ————, ————, and MIDUSIMA, U. A report on meiosis in the two hybrids, *Brassica alba* Rabh. ♀ × *B. oleracea* L. ♂ and *Eruca sativa* Lam. ♀ × *B. oleracea* L. ♂. Cytologia, Fujii Jub. Vol.: 437–441. 1937.
261. UPHOF, J. C. TH. On mendelian factors in radishes. Genetics **9**: 292–304. 1924.
262. VAARAMA, A. Chromosome number and cryptic polyploidy in *Lepidium sativum*. Hereditas **37**: 290–292. 1951. [Abst.]
263. VAN CLUTE, J. Caulicab is a new vegetable. Sowest. Crop & Stock **6**(3): 38–39. 1952.
264. VAVILOV, N. I. [Studies on the origin of cultivated plants.] Bull. Appl. Bot. and Plant Breed. **16**: 139–248. 1926.
265. VERSCHAFFELT, E. The causes determining the selection of food in some herbivorous insects. Kon. Akad. Wet. (Amsterdam), Proc. **13**(I): 536. 1910.
266. WALKER, J. C. Studies upon the inheritance of *Fusarium* resistance in cabbage. Phytopath. **16**: 87. 1926. [Abst.]
267. ————. Inheritance of *Fusarium* resistance in *cabb*age. Jour. Agr. Res. **40**: 721–745. 1930.
268. ————. Yellows-resistant lines of Jersey Wakefield cabbage. Jour. Agr. Res. **46**: 639–648. 1933.
269. ————. Resistance to clubroot in *Brassica*. Phytopath. **26**: 112. 1936. [Abst.]
270. ————. Resistance to clubroot in varieties of turnip and rutabaga. Jour. Agr. Res. **59**: 815–827. 1939.
271. ————. Progress in combination of yellows and mosaic resistance with ascorbic acid content in cabbage. Phytopath. **34**: 1012–1013. 1944. [Abst.]
272. ———— and FOSTER, R. E. The inheritance of ascorbic acid content in cabbage. Am. Jour. Bot. **33**: 758–761. 1946.
273. ———— and LARSON, R. H. Development of clubroot resistance in cabbage. Phytopath. **38**: 28. 1948. [Abst.]

274. ———— and ————. Progress in the development of clubroot-resistant cabbage. Phytopath. **41**: 37. 1951. [Abst.]
275. ———— and POUND, G. S. Improvement of cabbage for disease resistance. Phytopath. **37**: 23. 1947.
276. ———— and WELLMAN, F. L. A Fusarium-resistant cabbage of Jersey Wakefield type. Phytopath. **18**: 142. 1928. [Abst.]
277. ———— and ————. A survey of the resistance of sub-species of *Brassica oleracea* to yellows (*Fusarium conglutinans*). Jour. Agr. Res. **37**: 233–241. 1928.
278. WANG, T. M. Studies on the mechanism of resistance of cruciferous plants to *Peronospora parasitica*. Phytopath. **39**: 541–547. 1949.
279. WESTER, R. E., and MAGRUDER, R. Varietal and strain differences in bolting of turnips. Proc. Am. Soc. Hort. Sci. **35** (1937): 594–598. 1938.
280. WHEELER, L. C. The names of three species of *Brassica*. Rhodora **40**: 306–309. 1938.
281. WHITEHEAD, T. Experiments with "finger and toe" disease of swedes. Welsh Jour. Agr. **1**: 176–184. 1925.
282. WHITCOMB, W. D. Resistance of cabbage to cabbage maggot. Mass. Agr. Exp. Sta., Bull. 428: 39. 1945.
283. ————. Control of cabbage maggot. Mass. Agr. Exp. Sta., Bull. 436: 40. 1946.
284. YAKUWA, K. Cytological observations on autotetraploid *Brassica chinensis*. Cytologia **13**: 162–163. 1944.
285. YARNELL, S. H. Five abnormal types of cabbage. Proc. Am. Soc. Hort. Sci. **61**: 447–450. 1953.
286. YEAGER, A. F. The characteristics of crosses between botanical varieties of cabbage, *Brassica oleraceae*. Proc. Am. Soc. Hort. Sci. **43**: 199–200. 1943.
287. ZIMMERLEY, H. H. Cabbage strain tests. Va. Truck Exp. Sta., Bull. 37 and 38. 1922.
288. ZLATKOVSKY, A. [A hybrid between cauliflower and Brussels sprouts —a new form of vegetable in the making.] Sborn. Česk. Akad. Zeměd. **25**: 387–391. 1952. [Plant Breed. Abst. **23**: 1536. 1953.] [Original not seen.]

Future Contents of

THE BOTANICAL REVIEW

Articles Received and Awaiting Publication

A Guide to Literature on Ecology and Life Histories of Algae	G. W. Prescott *Michigan State College*
The Ecology of River Algae	John L. Blum *Canisius College*
Drought Resistance in Woody Plants	Johnson Parker *University of Idaho*
Fine Structure in Degraded, Ancient and Buried Wood, and Other Fossilized Plant Derivatives	J. Sen *Calcutta University*
The Plant Centrosome and the Centrosome-Blepharoplast Homology	Robert Lepper *University of Rhode Island*
Chromosomal Interchanges in Plants	C. R. Burnham *University of Minnesota*
Fixation of Plant Chromosomes: Principles, Limitations and Recent Developments	A. K. Sharma *Calcutta University*
Reproduction in the Bangiophycideae	Kathleen M. Drew *University of Manchester*
Colonization of Artificial Bare Areas by Microorganisms	Wm. Bridge Cooke *Dept. Health, Education and Welfare* *Cincinnati, Ohio*